

THE MORPHOLOGY AND SYSTEMATICS
OF THE AUDOUINELLA COMPLEX
(ACROCHAETIACEAE, RHODOPHYTA)
IN NORTHEASTERN UNITED STATES

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Our knowledge of the marine species of the *Audouinella* complex along the New England and adjacent coasts of North America (including New York and New Jersey) comes mainly from the papers of Collins (1906, 1908, 1911), Davis (1913), Farlow (1881), Harvey (1853), Hehre and Mathieson (1970), Jao (1936), and Woelkerling (1972). Although many of the earlier records (which leave a number of points to be clarified) are incorporated in the descriptive catalogues of Taylor (1937, 1957), a comprehensive morphotaxonomic study of New England marine audouinelloid algae has not appeared to date, and the only monographic attempt involving the New England species has been that of Collins (1906) which included all of North America and is now out of date.

The present account reviews the systematics, morphology, ecology, and distribution of New England marine audouinelloid algae and provides a taxonomic treatment of all representatives based on extensive field and herbarium studies including the examination of many of the type collections. Canadian representatives of the complex (see South and Cardinal, 1970) have not been considered in detail because of inadequate material and the questionable nature of a number of records. A brief discussion on these taxa appears at the end of this report.

The techniques employed in these studies have been detailed elsewhere (Woelkerling 1970, 1973). Abbreviations for herbaria follow Lanjouw and Stafleu (1964); collections designated by WJW refer to specimens in the author's personal herbarium, currently housed at WIS.

A comprehensive review of the taxonomic history of audouinelloid algae has appeared recently (Woelkerling

1971), and the systematic conclusions reached in that paper are supported and adopted here. D'Lacoste and Ganesan (1972), however, maintain a classification of genera based on chromoplast morphology and criticize the placement of *Rhodochorton* in synonymy with *Audouinella* on grounds that Woelkerling (op. cit.) did not examine chromoplasts in living material of *Rhodochorton purpureum*, the type species of *Rhodochorton*. Cells of living *R. purpureum* (referred here to *Audouinella*) have been examined during the present New England study and found to show the same variation in chromoplast morphology described by Drew (1928, pp. 156, 177, fig. 33).

D'LaCoste and Ganesan (1972, p. 235) also point out (citing the findings of West, 1968, p. 98) that chromoplast shape can change as a result of fixation of material and that studies on the latter (including, presumably, those of Drew, 1928) can yield misleading results. They apparently overlooked the other comments of West (op. cit.) in the same paragraph where he indicates the "... inadequacy of plastid form as a taxonomic criterion in certain instances ...". Thus the studies of West (1968), Woelkerling (1971), and others (see Woelkerling op. cit., p. 14) clearly show that chromoplast morphology is so variable in certain taxa that any generic segregation based on differences in plastid shape would result in a situation where certain species could be placed in several genera simultaneously. As a result, the present author has abandoned the use of chromoplast morphology as a generic criterion and has referred the genus *Rhodochorton* to the synonymy of *Audouinella*. For further comments, see the discussion of *A. purpurea* below and Woelkerling 1971, p. 4.

Taylor (1937, 1957) records 27 species in 5 genera from the northeastern coast of North America, all belonging to the family Acrochaetiaceae. (G. F. Papenfuss [personal communication] and P. C. Silva [personal communication] have indicated that the family name Acrochaetiaceae can be used correctly for the *Audouinella* complex even though the genus *Acrochaetium* is considered congeneric with

Audouinella; therefore the family name Audouinellaceae [Woelkerling 1971, p. 7, 22] is superfluous.)

Taylor's list may be enlarged to include the New England records of Giard (1890) and Hehre and Mathieson (1970) and the Canadian reports summarized by South and Cardinal (1970) to yield a total of 36 taxa for the region, apparently a greater number than in any other family of Rhodophyta. Of these, 29 are reported to occur in New England waters.

This account, however, recognizes only 11 species of audouinelloid algae as definitely occurring in New England; 7 of these are referred to the genus *Audouinella* and 4 to the genus *Colaconema*. Moreover, the names and (or) taxonomic status of all 29 taxa previously reported from New England have been changed; a summary appears in Table 1.

MORPHOTAXONOMIC FEATURES

The Acrochaetiaceae is generally circumscribed to include those Florideophycidae with simple or branched monosiphonous filaments usually less than 5 (rarely to 25) mm tall, with asexual reproduction by monospores, bispores, tetraspores, and/or multipartite spores, with carpogonia sessile on cells of vegetative filaments, intercalary in vegetative filaments or terminating one to several celled stalks, with gonimoblasts, when present, forming directly from the fertilized carpogonium, and without a pericarp. *Audouinella* Bory is the type genus.

Following Woelkerling (1971), the presence (*Audouinella*) or absence (*Colaconema*) of sexual reproduction is considered to provide a useful separation of the New England taxa into genera, with *Colaconema* regarded as a form genus similar to those of the Fungi Imperfecti. Taxa referable to *Kylinia* Rosenvinge (in its *original* sense) and *Liagorophila* apparently do not occur in New England, and the systematic status of these genera remains in doubt (see Woelkerling 1971, p. 6).

Within the genera *Audouinella* and *Colaçonema*, species have been grouped into three sections based on the absence of, the presence of one, or the presence of more than one pyrenoid per chromoplast. Species possessing more than one pyrenoid per chromoplast have not been collected in New England waters to date.

Additional features which appear to be of value in defining species limits include cell and spore dimensions, and in some cases chromoplast morphology, prostrate system morphology, and spore arrangement. Certain other characteristics (e.g. height of erect filaments, degree of branching, habitat preferences) sometimes are useful features for purposes of taxon recognition and in keys, but are too variable to be of value in defining species limits.

Considerable confusion has hitherto surrounded the identification of species in New England waters, and a number of records based on incorrect determinations have crept into and subsequently have been perpetuated in the literature. Thus, for example, collections originally identified by Collins (1906, 1911) as *Acrochaetium* (= *Chantansia*) *flexuosum* Vickers and subsequently recorded by Taylor (1937, 1957) have been re-examined during this study and found to belong unmistakably to *Colaçonema secundata*. Likewise collections hitherto referred to *Acrochaetium sagraeanum* involve at least three different audouinelloid taxa, and the type specimen itself is here excluded from the Rhodophyta (see "Species Excludendae").

To help minimize confusion of a similar nature in the future, the distinguishing features of each taxon known to occur in New England waters have been outlined at the onset of the discussion section of each species in the taxonomic accounts. Available distributional and ecological data are also included. While each species recognized here possesses a distinctive set of morphological features, most taxa exhibit considerable variation, and numerous plants of a collection should, therefore, be examined to build a composite picture of the population before identification is attempted. Collections of single specimens whose status is in doubt are best left unidentified.

KEY TO SPECIES OF NEW ENGLAND AUDOUINELLOID ALGAE

This key includes only species definitely known to occur in New England waters. Records of questionable occurrence, of taxa whose systematic status is uncertain, etc. are discussed in a separate section at the end of this report. Characters relating to chromoplasts and pyrenoids often are not preserved in dried or spirit material, and in these cases supplementary criteria are given in the key.

1. Multicellular prostrate system present; filamentous, parenchymatous, or pseudoparenchymatous. 2.
1. Multicellular prostrate system absent; plants attached to substrate by a single cell which may rarely give rise to one or several accessory cells. 7.
 2. Cells with a single chromoplast containing a single pyrenoid; plants generally (but not invariably) epiphytic or endophytic. 3.
 2. Cells with one to a number of chromoplasts without pyrenoids; plants generally (but not invariably) saxicolous or endozoic. 10.
3. Erect filaments generally over 500 μm long and usually exceeding the prostrate filaments in length; monosporangia commonly over 15 μm long. 4.
3. Erect filaments generally under 250 μm long or absent, usually shorter than or equal to the prostrate filaments; monosporangia under 15 μm long. 11.
 4. Chromoplasts distinctly stellate; prostrate system developing from an orbicular, parenchymatous group of cells which forms a small disc that may later proliferate and become obscured; lateral branches commonly but not always virgate or secundate. 11. *Colaconema secundata*.
 4. Chromoplasts parietal lobate curved plates; prostrate system filamentous or pseudoparenchymatous, not developing from a distinctive parenchymatous disc; lateral branches not virgate. 5.
5. Monosporangia borne, at least in part, in clusters of 3 or more on branched stalks. 4. *Audouinella daviesii*.

5. Monosporangia borne singly or in pairs but not in clusters. 6.
6. Prostrate system composed of an enlarged, central, more or less panduriform to pyriform cell and accessory cells or filaments which arise from it. 3. *Audouinella dasyae*.
6. Prostrate system filamentous or pseudoparenchymatous, without an enlarged, central panduriform or pyriform cell. 6. *Audouinella saviana*.
7. Cells commonly over 20 μm long; plants commonly over 500 μm tall. 8.
7. Cells under 20 μm long; plants rarely over 100 μm tall. 9.
8. Basal cell elongate, panduriform to pyriform; usually bearing accessory cells or filaments. 3. *Audouinella dasyae*.
8. Basal cell globose or subglobose; lacking accessory cells or filaments. 2. *Audouinella alariae*.
9. Cells commonly over 10 μm long; filament(s) of erect system procumbent; protoplast of basal cell hemispherical and distinctly flattened on side in contact with substrate. 7. *Audouinella unifila*.
9. Cells generally 10 μm or less long; filament(s) of erect system upright to arcuate; protoplast of basal cell more or less globose. 5. *Audouinella microscopica*.
10. Sporangia (i.e. carpotetrasporangia) borne mostly in clusters on branched stalk-like gonimoblast filaments; plants commonly but not invariably saxicolous. 1. *Audouinella purpurea*.
10. Sporangia (i.e. tetrasporangia) solitary, sessile or on unbranched stalks; plants commonly but not invariably endozoic. 8. *Colaconema membranacea*.
11. Cells commonly over 2 diameters long; prostrate filaments widely creeping, commonly over 1 mm long. 10. *Colaconema minima*.
11. Cells rarely over 2 diameters long; prostrate filaments rarely over 500 μm long. 9. *Colaconema humilis*.

AUDOUINELLA Bory

Audouinella Bory 1823: 340 (as *Auduinella*). Woelkerling 1971: 22. *Acrochaetium* Naegeli 1861: 402. *Balbiania* Sirodot 1876: 149. *Chromastrum* Papenfuss 1945: 320. *Grania* Kylin 1944: 26. *Rhodochorton* Naegeli 1861: 355. *Thamnidium* Thuret In Le Jolis 1863: 110. *Trentepohlia* Pringsheim 1862: 29.

Note: Species now referable to *Audouinella* have also been placed in the past in *Byssus*, *Callithamnion*, *Ceramium*, *Chantransia*, *Conferva*, *Kylinia*, and *Trentepohlia* Martius (1817). In addition, some species hitherto placed in *Acrochaetium*, *Audouinella*, *Callithamnion*, *Cermium*, *Chantransia*, *Chromastrum*, *Kylinia*, *Rhodochorton*, and *Trentepohlia* are referable here to the form genus *Colaconema*.

Plants epibiotic, endobiotic, or saxicolous; attached to or suspended in the substrate by a single basal cell, by a prostrate system of simple or branched filaments which may or may not become pseudoparenchymatous, or by a parenchymatous disc. Erect filaments simple or branched, up to 25 mm long; cells containing one to many variously shaped chromoplasts with or without pyrenoids.

Asexual reproduction by monosporangia, bisporangia, tetrasporangia, and/or multipartite sporangia; sporangia sessile or stalked and borne on erect or prostrate filaments.

Plants monoecious or dioecious. Spermatangia in clusters or occasionally single or in pairs, terminal or lateral on simple or branched stalks or sessile on ordinary vegetative cells. Carpogonia intercalary or more commonly sessile or terminating 1-2 celled stalks on vegetative cells, solitary or rarely in groups of 2-3; remaining undivided or dividing transversely after fertilization and giving rise directly to gonimoblast filaments bearing carposporangia or carpotetrasporangia.

Type Species: *Audouinella hermanni* (Roth) Duby.

Section I

Species in this section are not known to contain pyre-

noids in their chromoplasts. Within each section species are discussed in alphabetical order by specific epithet. Cell and spore dimensions are based only on the New England populations studied and may not reflect the total range of variation found in populations elsewhere. The ratio of greatest cell length to greatest cell diameter (width) is denoted by L/D in all species accounts.

1. **Audouinella purpurea** (Lightfoot) comb. nov. Figs. 52-55.

Byssus purpurea Lightfoot 1777: 1000.

Callithamnion purpureum (Lightfoot) Harvey 1841: 116, 1849: 183.

Conferva purpurea (Lightfoot) Dillwyn 1806: 56, pl. 43. C. Agardh 1817: XXIX.

Rhodochorton purpureum (Lightfoot) Rosenvinge 1900: 75. Collins, Holden, and Setchell 1895: 49. Conway and Knaggs 1966: 195 et seq., Figs. 1-3. DeToni 1903: 1510. Edelstein and McLachlan 1966a: 1041, 1052. Edelstein et al. 1970: 626. Hamel 1927: 57, 108; 1928: 201; 1928a: 151. Hehre and Mathieson 1970: 207. Knaggs 1965: 499 et seq., 1966b: 521 et seq., pl. 102-107; 1967: 139 et seq.; 1967a: 549 et seq., pl. 134-139; 1968: 449 et seq., pl. 170-174. Mathieson et al. 1969: 132. Papenfuss 1945: 327. South 1970: 1. South and Cardinal 1970: 2079. Stone et al. 1970: 325. Taylor 1957: 226, pl. 45, Figs. 1-2. West 1967: 11; 1969: 12 et seq., Figs. 1-22; 1970: 368 et seq., Figs. 1-8.

Trentepohlia purpurea (Lightfoot) C. Agardh 1824: 36. Harvey 1833: 382. Harvey and MacKay 1836: 218.

Rhodochorton islandicum Rosenvinge 1900: 75, Figs. 1-4. Papenfuss 1945: 327.

Rhodochorton intermedium (Kjellman) Kjellman 1883: 184, pl. 15, Fig 8. DeToni 1903: 1509. Hamel 1927: 107; 1928: 200.

Thamnidium intermedium Kjellman 1875: 28, Fig. 10.

Rhodochorton parasiticum Batters 1896: 389. Collins 1900: 51; 1900a: 12; 1911: 281. Collins, Holden and Setchell 1901: 848.

Callithamnion rothii (Turton) Lyngbye 1819: 129, pl. 41a. J. Agardh 1851: 17. Bailey 1847: 85. Collins 1880: 162. Eaton 1873: 348. Farlow 1875: 376; 1876: 704; 1879: 169; 1881: 121. Harvey 1846: pl. 120B; 1853: 243. Hay 1887: 66. Hay and MacKay 1888: 173. Jelliffe 1899: 15. Jordan 1874a: 488. Klugh 1917: 83. Kuetzing 1861: XI, pl. 621. Olney 1871: 8; 1872: 132. Pike 1886: 110.

Rhodochorton rothii (Turton) Naegeli 1861: 356, pl. 1, Figs. 1, 3. Bell and McFarlane 1933: 270. Boergesen 1902: 390, Figs. 61-64. Collins 1894: 230; 1900: 51; 1905: 234; 1911: 280; 1914: 4. Davis 1913: 818. DeToni 1903: 1507. Drew 1928: 177. Gibson 1891: 201, Fig. 38. Hamel 1927: 54, 106, Fig. 38; 1928: 199; 1928a: 147, Fig. 38. Hylander 1928: 169. Kjellman 1883: 185. Kuckuck 1897: 345, Fig. 5. Kylin 1944: 28, Fig. 25. Nakamura 1941: 282, Figs. 8-9. Rosenvinge 1923-24: 390, Figs. 328-330. Taylor 1937: 239, pl. 45, Figs. 1-2. Whelden 1947: 119.

Thamnidium rothii (Turton) Thuret In LeJolis 1863: 111, pl. 5.

Rhodochorton tenue Kylin 1925: 44, Figs. 25 b-e. Drew 1928: 177, pl. 40, Fig. 33. Papenfuss 1945: 328. West 1969: 12 et seq., Figs. 1-22.

Conferva violacea Roth 1797: 190, pl. 4, Fig. 1. Non *Conferva violacea* Hudson 1778: 592, nec *Ceramium violaceum* Roth 1797: 150, nec *Conferva rothii* Turton 1806: 1809.

Plants saxicolous or occasionally epibiotic, caespitose or forming conspicuous matted expanses with erect filaments up to 25 mm tall; original spore non-persistent. Prostrate system composed of branched, creeping filaments which may be loosely entangled or more compactly pseudoparenchymatous, but not forming distinct discoid holdfasts. Erect filaments moderately to freely and irregularly branched and usually tapering towards the tips. Cells cylindrical, 10-20 μm wide and 15-75 μm long, L/D (1-)2.5; tapering to 7-12 μm wide and 40-175 μm long (L/D up to 15) near and at the tips of branches; each cell containing

one to a number of irregularly lobate to reticulate to discoid chromoplasts without pyrenoids.

Monosporangia, bisporangia, parasporangia, and sex organs not observed. Carposporophytes consisting of short (up to 10 cells long), simple or usually branched gonimoblast filaments bearing terminal or occasionally lateral, ovoid, solitary or paired carpotetrasporangia 15-25 μm wide and 25-40 μm long. Other reproductive structures not observed.

Type Locality: Ruined Abbey, Island of Iona, Scotland.

Type: Possibly destroyed (see Conway and Knaggs 1966).

Distribution: Nearly cosmopolitan in temperate and polar marine waters; also known from terrestrial and freshwater sites.

Hosts: Most common on rocks but also on algae and invertebrates.

Specimens examined:

CONNECTICUT: Bridgeport (Harbor) 4. IX. 1893, *Johnson* (NY); 8. III. 1891, *Holden* (NY).

MAINE: Appledore Island (Isles of Shoals), 28. VII. 1938, *Croasdale* (NHA). Haley's Cove (Smuttynose Is., Isles of Shoals), 16. VI. 1966, *Shipman* (NHA). Harpswell, 6. VII. 1905, *Collins* (NY). Inner Mark Island, 29. VIII. 1903, *Collins* (NY). Lubec (Bailey's Mistake) 22 V. 1966, *Femino* (NHA). Lubec (West Quoddy Head), 21. V. 1966, *Ball* and *Lavise* (NHA). Peaks Island, VII. 1881, *Collins* (NY); 22. V. 1904, *Collins* (NY). Penobscot Bay, prior to 1853, *Hooper* (TCD). Popham, 7. VIII. 1900, *Chernington* (NY). South Harpswell, 17. VII. 1902, *Collins* (NY); 8. VII. 1903, *Collins* (NY). York (Nubble Light), 19. V. 1966, *Pollock* (NHA).

MASSACHUSETTS: Magnolia, 24. VI. 1896, *Collins* (NY). Nahant, 18. IV. 1879, *Collins* (?) (NY); 9. VI. 1889, *Collins* (NY); 30. III. 1890. *Collins*, (NY); 22. II. 1891, *Collins* (NY, = Collins, Holden, and Setchell 1895, No. 49); 30. V. 1900, *Collins* (NY, = Collins, Holden, and Setchell 1901, No. 848); 13. IV. 1907, *Collins* (NY). Penikese Island, 9. VII. 1926, *Taylor* (NY). Sandwich (jetty), 7. IV. 1968, *Kastelowitz* (NHA); 22. I. 1971, *Woelkerling* (WJW 3297). Scusset Beach, 7. IV. 1968, *Bosworth* (NHA); 29. III. 1969, *Mills* (NHA).

NEW HAMPSHIRE: Hampton, VIII. 1884, *Collins* (NY). North Wallis Sands, 16. VII. 1967, *Hehre* (NHA). Rye Ledge, 18. VIII. 1966, *Conway* and *Shipman* (NHA); 15. X. 1966, *Hehre* (NHA); 23. XII. 1966,

Conway and *Hehre* (NHA); 10. I. 1967, *Conway* and *Hehre* (NHA); 26. II. 1967, *Conway* and *Hehre* (NHA); 25. IV. 1967, *Hehre* (NHA); 25. V. 1967, *Hehre* (NHA); 22. VI. 1967, *Hehre* (NHA); 24. VII. 1967, *Hehre* (NHA); 12. VIII. 1967, *Mathieson* (NHA), 15. III. 1969, *Hutchinson* (NHA).

NEW JERSEY: Bay Ridge, 17. III. 1893, *Collins* (NY).

NEW YORK: Fort Hamilton (Long Island), 16. V. 1866, *Pike* (NY).

RHODE ISLAND: Newport, prior to 1853, *Bailey* (TCD).

Audouinella purpurea is distinguished from other New England audouinelloid algae in having a diphasic life cycle involving the production of carpotetraspores (Fig. 52) and in having erect filaments commonly over 10 mm long with cells containing 1 to a number of irregularly shaped to discoid chromoplasts without pyrenoids (Figs. 53-55). It is the only known New England species of audouinelloid algae which commonly develops on rocks and forms mat-like expanses.

A. purpurea grows throughout the year in New England and has been collected as far south as New Jersey. Most commonly it occurs in shaded habitats in the midlittoral, especially underneath *Ascophyllum* or *Fucus*, but it has been found throughout the intertidal and in the sublittoral zones. In sublittoral communities it apparently grows primarily as an epiphyte on kelp stipes. This species is widely distributed throughout the cooler regions of the northern hemisphere, and because it sometimes becomes an ecological dominant in the intertidal zone, it has been reported more frequently from northern regions than any other audouinelloid species.

Its vegetative morphology can vary considerably, depending upon the particular ecological niche it occupies, and this morphological variation has been the subject of intensive studies (*Conway* and *Knaggs* 1966; *Knaggs* 1965, 1966, 1966a, 1967, 1967a, 1968). In general, plants growing under stressed conditions tend to have shorter and less branched erect filaments. *Knaggs* (1965, 1966, 1966a) and *Conway* and *Knaggs* (1966) have recorded this species from freshwater and terrestrial habitats as well as intertidal and sublittoral habitats and have

recognized a number of distinct taxonomic forms. These forms, however, appear to have little taxonomic value in so far as New England populations are concerned and consequently are not recognized here as distinct systematic entities.

Reproductive structures have been found only in the winter and early spring; sterile plants, however, occur throughout the year. The latter bear some superficial resemblance to *Spermothamnion* but can easily be distinguished from that genus by the possession of a true heterotrichous habit. Sex organs have not been found in New England populations and to the author's knowledge have never been found in field collected samples. West (1969, 1970) has given an excellent account of these and other stages in the life history based on culture studies; Knaggs (1968) also reported sexual stages in cultural material. Mature carposporophytes are somewhat more loosely organized in comparison with other New England species and often greatly resemble ordinary vegetative branches bearing sporangia. Only carpotetrasporangia have been seen during this study, but bisporangia and parasporangia are reported from elsewhere (Conway and Knaggs, 1966; Knaggs, 1967).

Audouinella purpurea was the first described member of the *Audouinella* complex (Lightfoot, 1777), and because of its distinctiveness as a species (primarily in terms of habit and chromoplast morphology), it traditionally has been referred (as the type species) to a separate genus — *Rhodochorton* Naegeli (1861, p. 355). While recognizing its distinctness *as a species*, no reliable characteristics of generic significance (see Woelkerling 1971, p. 4) are apparent at present; consequently *Rhodochorton* is considered congeneric with *Audouinella*, and the type species, *R. purpureum*, is also referred to *Audouinella*.

Following Papenfuss (1945) and West (1969), the taxa originally described as *Rhodochorton parasticum* Batters (1869), *R. rothii* (Turton) Naegeli (1861), *R. tenue* Kylin (1925), and *Thamnidium intermedium* Kjellman (1875)

are here considered conspecific with *Audouinella purpurea*. In agreement with Conway and Knaggs (1966), *Rhodochorton islandicum* Rosenvinge is also regarded as conspecific with *Audouinella purpurea*.

Section II

Species in this section have chromoplasts with only one pyrenoid each.

2. *Audouinella alariae* (Jonsson) comb. nov. Figs. 1-9.

Acrochaetium alariae (Jonsson) Bornet 1904: XIX. Collins 1906: 192. Croasdale 1941: 214. Erskine 1955: 151. Hamel 1927: 84; 1928: 177. South 1970: 1. South and Cardinal 1970: 2079. Taylor 1937: 229.

Chantransia alariae Jonsson 1901: 132, Fig. 1. Adams 1904: 351. Boergesen 1902: 356. Boergesen and Jonsson 1905: Appendix, p. III. Collins 1911: 276. Cotton 1912: 98, 133. DeToni 1924: 45. Levring 1937: 86, Fig. 12.

Chromastrum alariae (Jonsson) Papenfuss 1945: 320.

Kylinia alariae (Jonsson) Kylin 1944: 13. Hehre and Mathieson 1970: 206. Mathieson et al. 1969: 132. Papenfuss 1947: 436. Taylor 1957: 213.

Acrochaetium rhipidandra (Rosenvinge) Hamel 1927: 25, 82, Fig. 23; 1928: 176; 1928a: 119, Fig. 23.

Chantransia rhipidandra Rosenvinge 1909: 91, Figs. 19-20. DeToni 1924: 37. Kylin 1928: 5, Figs. 1-2. Levring 1937: 83.

Chromastrum rhipidandra (Rosenvinge) Papenfuss 1945: 322.

Kylinia rhipidandra (Rosenvinge) Kylin 1944: 13. Papenfuss 1947: 437.

Rhodochorton rhipidandra (Rosenvinge) Drew 1928: 151.

Chantransia secundata auct. non. (Lyngbye) Thuret: Collins, Holden, and Setchell 1896a: 236. Collins 1900: 49 (pro parte).

Chantransia virgatula auct. non. (Harvey) Thuret: Collins 1894: 233 (Holden collection).

Plants epiphytic, up to 1.0 mm tall; original spore persisting as a globose to subglobose unicellular base up to 25 μm in diameter and usually larger than other cells. Basal cell bearing 1-2 (-3) erect filaments which are almost always branched; laterals irregularly arranged, few in number and nearly simple to numerous and frequently further subdivided; laterals generally tapering towards the tips. Cells cylindrical or occasionally somewhat barrel-shaped near the base, 12-18 μm wide and 15-60 μm long near the base, L/D (1-) 1.5-4; (4-) 7-10 (-15) μm wide and 15-65 μm long in the laterals, L/D 2-6 (-9); tapering to 4-9 μm wide near the tips; each cell containing a single chromoplast and one pyrenoid. Unicellular hairs not observed.

Monosporangia ovoid, 8-12 μm wide and 12-20 μm long, solitary or in pairs (occasionally in groups of 3), sessile or stalked, scattered to secundate along lateral branches or occasionally opposite or terminal on the branchlets.

Other reproductive structures not observed in New England collections.

Type Locality: The Maelstrom, Hvammsfjördur, Iceland.

Type: c (Jonsson 597).

Distribution: Northern Massachusetts northward; Denmark, Faeroes Islands, France, Great Britain, Iceland, Norway.

Hosts: *Alaria* in New England; *Alaria* and *Porphyra* in Europe.

Specimens examined:

MAINE: Bald Head Cliffs (Ogunquit), 17. VIII. 1966, *Shipman* and *Conway* (NHA); 7. XI. 1967, *Stone* and *Hehre* (NHA). Boon Island, 26. VII. 1938, *Croasdale* (NHA). Burnt Island (Cushing), 17. VII. 1888, *Collins* (NY). Cushing, no date, *Collins* (NY, Collins 446A). Casco Bay, VII. 1939, *Weatherhill* (FH). Hardhead Island (Penobscot Bay), VII. 1894, *Collins* (NY, loose duplicate of P.B.A. No. 236; FH, P.B.A. No. 236; WIS, P.B.A. No. 236). Mt. Desert Island, 12. VIII. 1890, *Holden* (NY, Holden 134). Nubble Light, 19. VIII. 1969, *Hehre* (WJW 2275). Pemaquid Point, 18. VII. 1901, *Collins* (NY). South Harpswell, 8. VII. 1903, *Collins* (NY).

MASSACHUSETTS: Pigeon Cove (Cape Ann), 25. IX. 1966, *Hehre* (NHA).

NEW HAMPSHIRE: Hampton, VII. 1894, *Collins* (NY); VIII. 1894, *Collins* (NY). Star Island (Isles of Shoals), 22. VII. 1966, *Conway* and *Shipman* (NHA).

CANADA: Ferryland, Avalon Penn., Newfoundland, 4. XII. 1968, *South* (CANA 7583). Ketch Harbor, Nova Scotia, 7. II. 1966, *Edelstein* (?) (Edelstein 2239, Herb. Nat. Res. Council, Halifax). Mulholland's Bend, Campebello Island, New Brunswick, 15. VI. 1967, *Hehre* and *Stone* (NHA).

DENMARK: Frederikshavn, Kattegat, 25. VIII. 1891, *Rosenvinge* (C, type of *Chantransia rhipidandra*).

ICELAND: The Maelstrom, Hvammsfjörður, 28. VI. 1897, *Jonsson* (C, *Jonsson* 597, type of *Audouinella alariae*).

Audouinella alariae is distinguished from other New England audouinelloid algae by the presence of a unicellular, more or less globose base (Figs. 1-3) bearing erect filaments whose cells are commonly over 2 diameters and 20 μ m long. It has been collected in New England from July through November on *Alaria esculenta* (L.) Greville, but also has been collected along the Canadian coast in February, June, and December. Further investigation may show that *Audouinella alariae* not only develops at other times of the year, but also grows on other substrates.

New England populations of *A. alariae* exhibit considerable morphological variation. Some mature plants reach heights of 1 mm while others never exceed 500 μ m. A few plants consisting of a single, nearly simple erect filament have been observed (Fig. 7), but in most cases lateral branches develop. The laterals themselves may be little further branched, long, and bear a few, scattered sporangia (Figs. 8-9), or they may be more densely subdivided, relatively short, and bear numerous, rather crowded sporangia (Figs. 4-5). All intermediate situations can occur within a single population.

Although pyrenoids have been observed during this investigation, the chromoplast shape could not be definitely determined. *Jonsson* (1901, p. 133) and *Levring* (1937, p. 87) both report a stellate chromoplast, but further study is needed to determine to what extent, if any, the plastid

shape might vary in this species. Collins (1906, p. 192) and Taylor (1937, p. 229; 1957, p. 213) report unicellular hairs, but such hairs have not been observed during this study and have not been recorded by other authors.

Collins (1906), Jonsson (1901), and Taylor (1937, 1957) report the monosporangia to be sessile and opposite; Adams (1904) records mostly alternate sporangia; and Levring (1937) states that the sporangia are often scattered. Plants in New England populations show a combination of all such arrangements on the same individual (Figs. 4, 5, 7-9), with oppositely arranged sporangia occurring only occasionally. They may be either sessile or on 1-2 celled stalks and sometimes terminate short lateral branches.

Critical comparisons (Table 2) of type collection material of *Audouinella alariae* and *Chantransia rhipidandra* Rosenvinge strongly indicate that the two taxa are conspecific. Rosenvinge (1909, p. 91) stated that *C. rhipidandra* differed from *Audouinella alariae* in ". . . having much thicker and more branched filaments, and further by the branches being often opposite . . ."; he also noted the presence of sex organs in the former and their absence in the latter.

However, plants examined during this study, including the types of both taxa, indicate considerable overlap in filament diameters (Table 2), and the degree of branching and branch arrangement (Figs. 4, 5, 7-9) vary considerably. Thus these criteria do not appear reliable for separating the two taxa. The presence or absence of sex organs alone also appears unreliable as a criterion of species separation (Woelkerling 1971), and since there appear to be no other criteria by which the two taxa can be reliably separated, they are regarded here as conspecific.

Hamel (1927, 1928), Kylin (1928), and Rosenvinge (1909) have described and illustrated sexual and carposporophyte stages of this species (all using the specific epithet "rhipidandra").

Chantransia unilateralis Kjellman (1906, p. 11, Taf. II, Figs. 1-4) is almost certainly conspecific with *Audouinella*

alariae, but the type collection of Kjellman's species apparently is not at UPS (personal communication), and final judgement must, therefore, be deferred until the type can be located and examined.

The relationships of *A. alariae* to at least 15 other taxa of similar morphology await clarification. Once critical examinations of all the types and other populations of these taxa are completed, it appears likely that a number will prove to be conspecific with *A. alariae*.

Specimens referred to *Chantransia secundata* by Collins (1900) and Collins et al. (1896a) and to *Chantransia virgatula* by Collins (1894) have been examined and found to contain only plants of *Audouinella alariae*. In the case of the former specimens, this confirms the opinions of Jonsson (1901) and Collins (1906).

Young plants of *Audouinella dasyae* bear many resemblances to *A. alariae* but usually can be recognized by the presence of a panduriform or pyriform basal cell rather than a globose one.

3. ***Audouinella dasyae*** (Collins) comb. nov. Figs. 10-31.

Acrochaetium dasyae Collins 1906: 191. Aziz 1967: 408. Davis 1913: 813. Edelstein et al. 1967: 195, Fig. 9. Hamel 1927: 77, 95, Figs. 47b-g; 1928: 171, 189, Figs. 47b-g. Papenfuss 1945: 308. Taylor 1937: 231; 1957: 217.

Chantransia dasyae (Collins) Collins 1911a: 186. DeToni 1924: 40.

Acrochaetium intermedium Jao 1936: 242, pl. 11, Figs. 1-4. Papenfuss 1945: 314. Taylor 1937: 231, pl. 33, Figs. 1-4; 1957: 218, pl. 33, Figs. 1-4.

Acrochaetium subseriatum Jao 1936: 243, pl. 11, Figs. 5-7 (Non *Acrochaetium subseriatum* Boergesen 1932: 118, Figs. 6-7). Taylor 1937: 232, pl. 33, Figs. 5-7.

Acrochaetium zosterae Papenfuss 1945: 307. Taylor 1957: 218, pl. 33, Figs. 5-7.

Callithamnion virgatulum auct non Harvey: Harvey 1853: 243.

Plants epiphytic, caespitose, up to 3 mm tall. Prostrate

system usually consisting of an enlarged, central, more or less panduriform to pyriform cell — the original spore — bearing several smaller accessory cells or short filaments; central cells becoming obscured by accessory filaments in robust plants or rarely remaining unicellular in young or small plants. Erect filament(s) arising from the central cell, moderately to freely and irregularly branched; sometimes tapering towards the tips. Cells cylindrical, 25-70 (-90) μm long and 7-12 (-16) μm wide [L/D 2-6 (-10)] in main axes, 15-60 μm long and 6-10 μm wide (L/D 2-7) in the laterals; each containing a single parietal chromoplast with one pyrenoid. Unicellular hairs not observed.

Monosporangia ovoid, 16-24 μm long and 9-12 (-16) μm wide, solitary or occasionally in pairs, sessile or occasionally stalked, in secundate series along the laterals or more scattered. Bisporangia and tetrasporangia not observed.

Spermatangia globose to ovoid, up to 3 μm wide and 5 μm long, borne terminally or laterally on vegetative cells or unicellular stalks, or usually in clusters of varying size on multicellular simple or branched stalks. Carpogonia sessile or stalked, scattered over the lateral filaments; fertilized carpogonium dividing transversely and eventually giving rise to a branched gonimoblast bearing terminal carposporangia 16-24 μm wide and 9-12 μm long.

Type locality: Woods Hole, Massachusetts.

Type: FH (accompanied by a card in Collins script and numbered 5370). Isotypes have been distributed as No. 1342 in *Phycotheca Boreali Americana* (Collins, et al. 1906).

Distribution: Atlantic Coast of North America.

Hosts: *Dasya* (Rhodophyta) and *Zostera* (Angiospermae).

Specimens examined:

MASSACHUSETTS: Edgartown (Martha's Vineyard), 19. XII. 1969, *Woelkerling* (WJW 2245). Great Rip (1.25 km E. of Great Point, Nantucket Is.), 14. IV. 1970, *Woelkerling* (WJW 2500). North Eastham, 9. VIII. 1959, *Lamb* (FH, filed under the host, *Dasya pedicel-*

lata). Old Silver Beach, 31. X. 1970, *Woelkerling* (WJW 2853); 15. XI. 1970, *Woelkerling* (WJW 2856); 30. XII. 1970, *Woelkerling* (WJW 2977). Waquoit Bay (Falmouth), 16. X. 1969, *Conway* (WJW 2293); 27. IV. 1970, *Woelkerling* (WJW 2534). West Falmouth Harbor, 6. I. 1970, *Woelkerling* (WJW 2284); 18. VII. 1970, *Woelkerling* (WJW 2751). West Yarmouth, 17. IX. 1969, *Woelkerling* (WJW 2252); 3. X. 1969, *Woelkerling* (WJW 1852), (WJW 2255); 16. XI. 1969, *Woelkerling* (WJW 2249), (WJW 2250); 12. XII. 1969, *Woelkerling* (WJW 2260). Woods Hole, 12. VIII. 1894, *Holden* (FH, filed under the host, *Dasya pedicellata*); 2. IX. 1905, *Collins* (FH, type); 29. VIII. 1944, *Taylor* (FH, filed under the host, *Dasya pedicellata*); 4. II. 1970, *Woelkerling* (WJW 2330); 5. VII. 1970, *Wilce* (WJW 2690); 17. VII. 1970, *Woelkerling* (WJW 2716); 13. X. 1970, *Woelkerling* (WJW 2820); 29. I. 1971, *Woelkerling* (WJW 3298); 16. II. 1971, *Woelkerling* (WJW 3311); 25. VIII. 1933, *Jao* (MICH, Woods Hole No. 278, type of *Acrochaetium zosterae* Papenfuss). Pine Island (Woods Hole), 7. VIII. 1934, *Jao* [MICH, Woods Hole No. 277, type of *Acrochaetium intermedium* Jao, non *Thamnidium intermedium* Kjellman = *Audouinella purpurea* (Lightf.) comb. nov.].

NEW JERSEY: Great Bay (.4 km SSW of Wells Is.), 17. VII. 1963, *Moeller* (RUT, filed under the host, *Dasya pedicellata*).

NEW YORK: Hell Gate (Long Island), 29. IX. 1850, *Walters* (TCD).

CANADA: Malpeque Bay (Prince Edward Island), 5. VIII. 1966, *Edelstein* (Nat. Res. Coun. Herb., Halifax).

Audouinella dasyae is distinguished from other New England audouinelloid algae by the presence of an enlarged, central, more or less panduriform to pyriform cell in the prostrate system (Figs. 12-17) which bears accessory prostrate cells or filaments and which gives rise to the erect filaments. *A. dasyae* appears to be confined to the sublittoral and has been collected in New England all months except March, May, and June. It undoubtedly occurs throughout the year. Sexual plants have been found from July through November; tetrasporangial plants have not been observed but probably occur and are to be expected in deeper waters in late spring and early summer.

Like many audouinelloid algae, *A. dasyae* exhibits considerable variation [more than indicated by Collins (1906) or Taylor (1957)] in cell width, height, spore size, and other features. On *Dasya* for example, it is not uncommon to find mature plants under 500 μ m tall anchored to the monosiphonous filaments of the host and plants up to

3 mm attached to the more robust multilayered primary axes of the the host. Likewise branching of *A. dasyae* may be dense or relatively sparse (Figs. 20, 21), depending upon the "growing room" available. In all cases the enlarged central cell representing the original spore was panduriform or pyriform; globose cells described by Taylor (1957) and illustrated by Hamel (1927, Fig. 47b; 1928, Fig. 47b) have not been observed except in sporelings (Figs. 10-11). In addition, the range of cell and spore dimensions recorded during this study are considerably greater than those reported by Collins (1906) or Taylor (1937, 1957).

Sexual plants have been reported before only by Aziz (1967). Spermatangial clusters vary considerably in size both within and between populations. In some cases the cluster is densely branched and bears numerous spermatangia, while in others it remains small, and in some cases spermatangia are even borne directly on vegetative cells or on unicellular stalks (Figs. 29-31).

It appears that the trichogynes of unfertilized carpogonia continue to elongate until a spermatium lands on the tips (Fig. 22). Only several fertilized carpogonia with clear transverse divisions have been observed (Fig. 25), and further study is needed to determine whether gonimoblast cells are cut off without such a division first occurring.

Critical comparisons of the type and other collections of *Audouinella dasyae*, *Acrochaetium intermedium* Jao (1936, p. 242, pl. 11, Figs. 1-4), and *Acrochaetium zosterae* Papenfuss (1945, p. 307 = *A. subseriatum* Jao 1936, p. 243, pl. 11, Figs. 5-7, non *A. subseriatum* Boergesen 1932, p. 118) indicates that all three taxa are conspecific (Table 3).

Jao (1936, p. 243) distinguished *A. intermedium* from *Audouinella dasyae* on the bases of an elongate rather than globose central cell, the presence of endophytic prostrate filaments, longer cells, more extensive branching, and the presence of bisporangia. However, all collections of *A. dasyae* examined, including the type, have panduriform or pyriform central cells at maturity, may or may not

produce accessory prostrate filaments, have cells of similar dimensions (Table 3), and contain plants with varying degrees of branching. Bisporangia have not been observed in the type collection material of *A. intermedium* examined during this study; however, the presence or absence of bisporangia (possibly incompletely divided tetrasporangia) alone does not warrant specific distinction (Woelkerling 1971). Since no other reliable distinguishing criteria could be found, the two taxa are considered conspecific. Aziz (1967) previously proposed that the two entities belonged to the same species.

Acrochaetium zosterae reportedly (data from Jao 1936, p. 244) differs from *Audouinella dasyae* in the shape of the central cell and in the larger size of monosporangia. Central cell shape of the two taxa is essentially the same (see above), and an examination of type material of *Acrochaetium zosterae* indicates that most monospores are 18-24 μm long and 8-11 μm wide rather than 22-31 μm long and 6.5-9.5 μm wide as reported by Jao (1936). The first set of dimensions falls within the range found for other New England populations of *Audouinella dasyae*. Since differences in host (*Dasya* vs. *Zostera*) are not taxonomically reliable (Woelkerling 1971) and since no other reliable criteria could be found to distinguish the two taxa, they are also considered conspecific.

Acrochaetium opetigenum Boergesen (1915, p. 38, Figs. 35-37), *A. robustum* Boergesen (1915, p. 40, Figs. 38-40), and *A. unipes* Boergesen (1915, p. 35, Figs. 31-35) are very similar to *Audouinella dasyae*, and a comparative examination of the type collections will probably show that all are conspecific. Boergesen (1915) separated all of these taxa on slight differences in prostrate system structure, but none appears to be taxonomically reliable (see Woelkerling 1971).

The relationships between *A. dasyae* and *Chantransia macounii* Collins (1913, p. 113) require further clarification. Collins (1913) states in the original description that the cell representing the original spore does not remain

distinct; Drew (1928, p. 184, pl. 43, Figs. 47-52, pl. 44, Fig. 53), however, describes and illustrates a distinct central cell which she says becomes obscured by other prostrate filaments. Both Drew's material and the type collection of Collins need to be re-examined and compared with *Audouinella dasyae* to determine whether any or all are conspecific.

Collins (1906, p. 192) suspected that specimens of Harvey (1853, p. 243) collected at Hell Gate, Long Island, New York in 1850 and referred to *Callithamnion virgatulum* Harvey were in reality plants of *Audouinella dasyae*. Harvey's original material from TCD has been examined and indeed contains only plants of *A. dasyae*, as suspected by Collins.

As noted previously, young plants of *A. dasyae* can under some circumstances become confused with specimens of *A. alariae*. The two can usually be distinguished on differences in basal cell shape.

4. ***Audouinella daviesii*** (Dillwyn) Woelkerling 1971: 28, Figs. 7, 22; 1973: 81. Figs. 32-43.

Acrochaetium daviesii (Dillwyn) Naegeli 1861: 405, Figs. 26-7. Baardseth 1941: 42, Fig. 18. Collins 1906: 194 (?); 1908: 134. Davis 1913: 813. Doty 1948: 263. Edelstein et al. 1970: 634. Hamel 1927: 39, 98, Fig. 31; 1928: 192; 1928a: 133, Fig. 31. South and Cardinal 1970: 2079. Taylor 1937: 234, pl. 31., Figs. 8-10; 1957: 221, pl. 31, Figs. 8-10.

Callithamnion daviesii (Dillwyn) Lyngbye 1819: 129 (only as to binomial). J. Agardh 1851: 11; 1876: 8. Jordan 1874: 197; 1874a: 488.

Ceramium daviesii (Dillwyn) C. Agardh 1817: XXVII.

Chantransia daviesii (Dillwyn) Thuret In LeJolis 1863: 106. Collins 1880: 162 (?); 1894: 233 (?); 1900: 49 (?); 1911: 276 (?). DeToni 1897: 67; 1924: 55. Farlow 1875: 376; 1876: 705. Kylin 1907: 117, Fig. 27. Rosenvinge 1909: 104, Fig. 34.

Conferva daviesii Dillwyn 1809: 73, Suppl. pl. F.

Rhodochorton daviesii (Dillwyn) Drew 1928: 172. Nakamura 1944: 106, Fig. 5.

Trentepohlia daviesii (Dillwyn) Areschoug 1847: 338. Farlow 1881: 109. Martindale 1889: 100.

Acrochaetium amphiroae (Drew) Papenfuss 1945: 312. Doty 1948: 263. Edelstein and McLachlan 1968: 993, Figs. 49-50 (?). Mathieson et al. 1969: 131. South 1970: 1. South and Cardinal 1970: 2079. Taylor 1957: 223.

Rhodochorton amphiroae Drew 1928: 179, pl. 40, Figs. 34-37.

Acrochaetium alcyonidii Jao 1936: 245, pl. 12, Figs. 2-4. Papenfuss 1945: 312. Taylor 1937: 234, pl. 34, Figs. 2-4; 1957: 200, pl. 34, Figs. 2-4.

Acrochaetium alcyonidii Jao var. *cylindricum* Jao 1936: 245, pl. 12, Fig. 5. Taylor 1937: 234, pl. 34, Fig. 5; 1957: 221, pl. 34, Fig. 5.

Acrochaetium sagraeanum auct. non. (Montagne) Bornet: Boergesen 1915: 35 (pro parte). Bornet 1904: XXI (pro parte). Collins 1906: 192 (pro parte). Hamel 1927: 77, 99 (pro parte); 1928: 173, 191 (pro parte). Jao 1936: 244 (pro parte). Papenfuss 1945: 311 (pro parte). Taylor 1960: 309 (pro parte). Vickers 1905: 60.

Chantransia sagraeana auct. non. (Montagne) DeToni: DeToni 1924: 51 (pro parte).

Chantransia corymbifera auct. non. Thuret In LeJolis (pro parte; see Papenfuss 1945, p. 313 under *Acrochaetium bornetii*): Collins 1896: 5. Collins, Holden, and Setchell 1896: 192.

Chantransia efflorescens var. *thuretii* auct. non. Bornet: Collins 1906: 196. Davis 1913: 813.

Acrochaetium thuretii auct. non. (Bornet) Collins et Hervey: Taylor 1937: 236; 1957: 222.

Note: Additional synonymy is presented by Woelkerling (1971).

Plants partly to entirely epiphytic or epizoic, caespitose, up to 6 mm tall; original spore non-persistent. Prostrate system consisting of branched epi- or endophytic or epi- or endozoic filaments forming a pseudoparenchymatous

disc or an entangled funiform mass. Erect filaments moderately to freely and irregularly branched, sometimes tapering towards the tips or attenuate and ending in multicellular hair-like prolongations. Cells cylindrical, (6-) 9-12 (-20) μm wide and (8-) 15-50 (-70) μm long, L/D (1-) 2-4 (-6) in main axes and laterals; about 4 μm wide and up to 75 μm long in hair-like prolongations; each cell containing a single parietal lobate chromoplast with one pyrenoid.

Monosporangia ovoid, 7-13 μm wide and (8-) 12-20 μm long, in clusters of 3 or more on branched stalks or singly or in pairs on 1-2 celled stalks, situated on the lowermost cells of laterals or sometimes more scattered. Tetrangia ovoid, 16-22 μm wide and 24-36 μm long, borne in pairs on unicellular stalks or occasionally solitary or in groups of 3, situated on the lowermost cells of laterals or more scattered.

Spermatangia ovoid to spherical, up to 4 μm wide and 5 μm long, borne terminally or laterally in small clusters on branched stalks. Carpogonia terminal on unicellular stalks; immediate post-fertilization stages not observed. Mature carposporophyte consisting of branched gonimoblast filaments bearing terminal, ovoid carposporangia 9-18 μm wide and 18-26 μm long.

Type Locality: Bantry Bay, Ireland (Hutchens); locality for H. Davies collection not given by Dillwyn (1809).

Type: NMW.

Distribution: Nearly cosmopolitan.

Hosts: A wide variety of algae, and invertebrates.

Specimens examined:

MAINE: Eastport, 1873, *Averill* (?) (NY).

MASSACHUSETTS: Gay Head (Martha's Vineyard), VIII. 1875, *Farlow* (FH); (NY). Gloucester, IX. 1878, *Farlow* (FH). Marblehead, 16. IX. 1888, *Collins* (NY); 27. VIII. 1895, *Collins* (NY). Nantucket Center (Nantucket Is.), 14. IV. 1970, *Woelkerling* (WJW 2577). Old Silver Beach, 31. X. 1970, *Woelkerling* (WJW 2855); 30. XII. 1970, *Woelkerling* (WJW 2978), (WJW 2976). Salisbury Beach, 31. V. 1909, *Collins* (?) (NY). Waquoit (Harbor Entrance), 27. IV. 1970, *Woelk-*

erling (WJW 2536). West Falmouth Harbor, 3. X. 1970, *Woelkerling* (WJW 2769). West Yarmouth, 16. XI. 1969, *Woelkerling* (WJW 2248). Woods Hole (Butlers Point), 15-20. VII. 1895, *Nott* (FH [P.B.A. 192], NY, WIS [P.B.A. 192]). Woods Hole (Nobska Point), 4. II. 1970, *Woelkerling* (WJW 2332), (WJW 2322); 2. VII. 1970, *Woelkerling* (WJW 2678); 17. VII. 1970, *Woelkerling* (WJW 2719); 29. I. 1971, *Woelkerling* (WJW 3302); 12. II. 1971, *Fiore* (WJW 3320); 16. II. 1971, *Woelkerling* (WJW 3314). Woods Hole (Pine Island), 9. VII. 1938, *Taylor* (NY). Woods Hole (Sheep Pen Harbor), 1. IX. 1934, *Jao* (MICH, apparently a portion of type collection of *Acrochaetium alcyonidii* Jao).

NEW YORK: Montauk Point (Long Island), 20. I. 1970, *Woelkerling* (WJW 2198).

CANADA: Paddy's Head (Nova Scotia), 13. X. 1965, *Edelstein* (Herb Nat. Res. Council, Halifax, 2110).

IRELAND: Bantry Bay, prior to 1809, *Hutchins* (NMW, Dillwyn collection, type).

Audouinella daviesii is distinguished from other New England audouinelloid algae by the arrangement (at least in part) of monosporangia in clusters of 3 or more on branched stalks which are usually situated on the lowermost cells of lateral branches (Figs. 32-35). On some plants all monosporangia are borne in such clusters while on others, notably sexual and tetrasporangial plants, clustered monosporangia may not be very evident or numerous.

A. daviesii appears to be mainly a sublittoral plant although several populations have been found on *Fucus* in the lowermost littoral. It has been collected in New England in all months except March and June, but almost certainly occurs throughout the year. Sexual plants have been collected in July, August, and September (WJW 2678, FH, NY); tetrasporangial plants have appeared in January (WJW 2198).

The vegetative appearance of *Audouinella daviesii* varies considerably. When growing on *Codium*, for example, the prostrate system becomes an endophytic funiform mass of filaments lodged between the utricles of the host. When growing on *Chondria*, in contrast, the prostrate system forms an epiphytic pseudoparenchymatous disc. Similar variation has been found in Australian populations of *A. daviesii* (Woelkerling 1971). Intergrades between these

forms also occur. The ratio of cell length to cell diameter also shows considerable variation. In some populations, most plants have cells with an L/D over 3 (Fig. 32) while in other populations, the ratio of cell length to cell diameter is almost always less than 3 (Fig. 33). Intergrades always occur, and sometimes transitions from short cells to longer cells can be found along single filaments (Fig. 34).

Other vegetative features which vary include the degree of branching and the occurrence of multicellular hair-like prolongations. In some plants the degree of branching is only moderate; laterals arise at infrequent intervals and are little further divided. In other plants, however, branching is abundant and laterals often arise in groups in close proximity to one another in a more or less fasciculate manner. Hair-like prolongations occur in some populations but not in others. Often these prolongations were broken off giving the lateral branches a stubby appearance.

Several sexual and one tetrasporangial collection have been made in New England waters to date. Unfortunately, immediate post-fertilization stages have still not been observed (see Woelkerling 1971) and it is not known whether the fertilized carpogonium divides transversely, longitudinally, or gives rise directly to gonimoblast filaments. Carposporangia in the New England populations tend to be larger than those found in Australia (Woelkerling 1971).

Acrochaetium alcyonidii Jao (1936, p. 245, pl. 12, Figs. 2-4) and *A. alcyonidii* var. *cylindricum* Jao (1936, p. 245, pl. 12, Fig. 5) are here considered conspecific with *Audouinella daviesii*. Two slides labelled "alcyonidii" by Jao in MICH, which are presumably from the original collection but do not bear the number Woods Hole 279 (see Jao 1936, p. 245), have been examined and found to contain only the basal portions of several plants without any monosporangia or other reproductive structures. Thus the material is unidentifiable.

The published accounts and illustrations of Jao (1936) and Taylor (1937, 1957) leave little doubt about the con-

specificity of *Acrochaetium alcyonidii* and *Audouinella daviesii*. Jao (1936) separated the former from the latter "... in having a strongly marked endozoic habit and very short lateral branches." However, host differences, habit, and length of lateral branches appear to be of little taxonomic significance (Woelkerling 1971). Moreover several New England populations (Taylor, Pine Island Coll. in NY; WJW 3320) growing on *Alcyonidium* (the host of *Acrochaetium alcyonidii*) have been examined and found to agree in all essential respects with *Audouinella daviesii*. In light of these considerations, and because no other criteria of taxonomic significance are apparent (the presence of bisporangia, reported by Jao (1936) but not seen during this study, does not alone appear to be sufficient grounds for species separation), *Audouinella daviesii* and *Acrochaetium alcyonidii* are considered conspecific.

Acrochaetium amphiroae (Drew) Papenfuss has already been referred to the conspecificity of *Audouinella daviesii* (Woelkerling 1971); consequently the records of Doty (1948), Mathieson *et al.* (1969), South (1970), and Taylor (1957) are referred (at least as to name) to *A. daviesii*. None of the collections upon which these records are based, however, has been available for examination.

A number of collections of other investigators have been examined and apparently found not to contain plants of *A. daviesii*. Specimens which Harvey (1853, p. 243) referred to *Callithamnion daviesii* belong to *Colaconema secundata*. With one exception (see specimens examined listing), all the collections of Collins examined, both in FH and NY, including *Phycotheca Boreali Americana* Specimen No. 880, have been found not to contain plants of *A. daviesii* but rather plants referable to *Colaconema secundata*. Since there is a slight possibility that both taxa are present in Collins material, Collins references are listed with question marks in this account. The uncertainty over Collins material leads to uncertainty over the reported distribution of *A. daviesii* in the New England region; in addition to a number of stations in Massachu-

setts, *A. daviesii* is also definitely known from only one locality in Maine and one in New York as a result of the present study.

Plants from Nova Scotia referred to *Acrochaetium alcyonidii* (Edelstein *et al.* 1967) and *A. amphiroae* (Edelstein and McLachlan 1968) should be checked; one collection sent from Dr. Edelstein and identified as *A. alcyonidii* has been examined and found to contain only plants of *Colaonema membranacea* (Magnus) comb. nov. Likewise, the illustrations (Edelstein and McLachlan 1968, Figs. 49-50) of plants referred to *Acrochaetium amphiroae* leave considerable doubt as to their true relationship to *Audouinella daviesii*.

A number of specimens hitherto referred to *Acrochaetium sagraeanum* (Montagne) Bornet have been examined and found to be *Audouinella daviesii*; citations are appended. The type of *Acrochaetium sagraeanum* has been excluded from the Rhodophyta (see "Species Excludendae").

Massachusetts specimens collected by Collins in 1888 and 1895 from Marblehead, by Farlow in 1875 from Gay Head (Martha's Vineyard; host is *Cystoclonium*), and by Nott in 1895 from Butler's Point (Woods Hole) in FH and NY have been examined during this study and found to contain sexual plants of *Audouinella daviesii* and, in several instances, a plant or two of *Colaonema secundata*. In the literature, these collections have been referred erroneously to *Chantransia corymbifera* (Collins 1896; Collins, Holden, and Setchell 1896, No. 192), *C. efflorescens* var. *thuretii* (Collins 1906, Davis 1913), and/or *Acrochaetium thuretii* (Taylor 1937, 1957). The vast majority of plants examined in the above populations contained numerous carposporophytes and very few monosporangia. In each case, however, the few monosporangia found tended to be arranged in axial clusters of 3-4 on branched stalks, and this is the characteristic arrangement found in *Audouinella daviesii*. In other respects these populations agree well with sexual plants collected during this study. For

additional information, see comments below under *Audouinella efflorescens*.

5. **Audouinella microscopica** (Naegeli In Kuetzing) Woelkerling 1971: 33, Figs. 10, 23A. 1972: 85 et seq., Figs. 1-14; 1973: 86. Figs. 46-51.

Acrochaetium microscopicum (Naegeli In Kuetzing) Naegeli 1861: 407, Figs. 24-25.

Callithamnion microscopicum Naegeli In Kuetzing 1849: 640.

Chantransia microscopica (Naegeli In Kuetzing) Batters In Schiffner 1916: 136, Figs. 13-18.

Chromastrum microscopicum (Naegeli In Kuetzing) Papenfuss 1945: 322.

Kylinia microscopica (Naegeli In Kuetzing) Kylin 1944: 13. Papenfuss 1947: 437.

Rhodochorton microscopicum (Naegeli In Kuetzing) Drew 1928: 151, 163.

Acrochaetium catenulatum Howe 1914: 84, pl. 31, Figs. 12-18.

Chantransia catenulata (Howe) DeToni 1924: 44.

Kylinia catenulata (Howe) Kylin 1944: 13.

Rhodochorton catenulatum (Howe) Nakamura 1941: 273, 280, Fig. 1.

Acrochaetium collopodum (Rosenvinge) Hamel 1927: 81; 1928: 175.

Chantransia collopoda (Rosenvinge) Rosenvinge 1909: 81.

Chromastrum collopodum (Rosenvinge) Papenfuss 1945: 320.

Kylinia collopoda (Rosenvinge) Kylin 1944: 13, 15, Fig. 6.

Acrochaetium compactum Jao 1936: 241, pl. 10, Figs. 6-14. Taylor 1937: 228, pl. 32, figs. 6-14.

Chromastrum compactum (Jao) Papenfuss 1945: 321.

Kylinia compacta Papenfuss 1947: 436. South 1970: 1. Taylor 1957: 212, pl. 32, Figs. 6-14.

Acrochaetium crassipes (Boergesen) Boergesen 1915: 20, Figs. 11-13. Boergesen 1927: 12, Fig. 5. Collins and

Hervey 1917: 96. Howe 1918: 511. Taylor 1941: 75.

Chantransia crassipes Boergesen 1909: 1, Fig. 1. Taylor 1928: 134, pl. 28, Fig. 16.

Chromastrum crassipes (Boergesen) Papenfuss 1945: 321.

Kylinia crassipes (Boergesen) Kylin 1944: 13. Taylor 1960: 300.

Acrochaetium microfilum Jao 1936: 240, pl. 10, Figs. 1-5. (Non *A. microfilum* Levring 1945: 12, Fig. 4. = *A. levrिंगii* Papenfuss 1947: 436). Taylor 1937: 232, pl. 32, Figs. 1-5; 1957: 219, pl. 32, Figs. 1-5.

Acrochaetium moniliforme (Rosenvinge) Boergesen 1915: 22. Jao 1936: 241, pl. 10, Figs. 15-17. Taylor 1937: 227, pl. 32, Figs. 15-17.

Chantransia moniliformis Rosenvinge 1909: 99, Figs. 28-29.

Chromastrum moniliforme (Rosenvinge) Papenfuss 1945: 322.

Kylinia moniliformis (Rosenvinge) Kylin 1944: 13. South 1970: 1. Taylor 1957: 211, pl. 32, Figs. 15-17.

Rhodochorton moniliforme (Rosenvinge) Drew 1928: 151, 164.

Chantransia secundata auct. non. (Lyngbye) Thuret: Hauck and Richter 1892: 454.

Plants epiphytic, up to 100 μm tall exclusive of hairs; original spore persisting as a unicellular base slightly smaller to slightly larger than other cells. Filaments of erect system 1-4, commonly arcuate, simple or with a few secundly to irregularly arranged lateral branches. Cells barrel-shaped to cylindrical, 3-10 μm wide and 3-11 μm long, L/D 0.75-2; each cell containing a single parietal lobate to stellate chromoplast with one pyrenoid. Terminal hairs up to 40 μm long occur occasionally.

Monosporangia ovoid, 4-9 μm wide and 6-15 μm long. terminal or lateral, single or rarely in pairs, sessile or stalked, adaxially seriate or occasionally more scattered.

Other reproductive structures not observed in New England populations.

Type locality: Torquay, England.

Type: L, No. 940285 . . . 306.

Distribution: Nearly cosmopolitan.

Hosts: *Chaetomorpha*, *Chordaria*, *Cladophora*, *Enteromorpha*, *Polysiphonia*, and *Sphaerotrichia* in New England; a wide variety of algae and bryozoans elsewhere.

Specimens examined:

MASSACHUSETTS: Black Rock, Sconticut Neck, New Bedford, 25. VII. 1934, Jao (MICH, Woods Hole, No. 275, type of *Acrochaetium compactum* Jao). Cape Codder Point, Falmouth 19. XI. 1969, Woelkerling (WJW 2292). Norton Point, Martha's Vineyard, 3. VIII. 1934, Jao (MICH, Woods Hole, No. 280 [not 274 as reported by Jao 1936, p. 240], type of *Acrochaetium microfilum* Jao). West Falmouth Harbor, 17. X. 1970, Woelkerling (WJW 2826). Woods Hole (Nobska Point), 4. II. 1970, Woelkerling (WJW 2320).

ENGLAND: Torquay, 1845, Naegeli (L 940285 . . . 306, type of *Audouinella microscopica* (Naegeli) Woelkerling). Torquay, 1845, Naegeli (FH = Hauck and Richter 1892, No. 454, isotype of *A. microscopica*, which is labeled *Chantransia secundata*). Torquay, 1845, Naegeli (NY = Hauck and Richter 1892, No. 454, isotype of *A. microscopica*, which is labeled *Chantransia secundata*).

Audouinella microscopica is distinguished from other New England audouinelloid algae with a unicellular base 1) in commonly having cells isodiametric or broader than long; 2) in having a more or less globose basal cell protoplast that is not markedly flattened on the side in contact with the substrate; and 3) in having erect or ascending rather than procumbent filaments.

A detailed morphotaxonomic account of this species in New England and adjacent regions has recently appeared in the literature (Woelkerling 1972). To date this species has been collected only from Massachusetts along the New England coast, but it is known from Nova Scotia (Edelstein and McLachlan 1966, 1968; Edelstein et al. 1967; South and Cardinal 1970) and, therefore, is to be expected at intermediate points. Although collection data is incomplete, *A. microscopica* probably is present throughout the year and is to be sought on any older, epiphytized algae. Its microscopic size may account for its being generally overlooked.

6. *Audouinella saviana* (Meneghini) comb. nov. Figs. 56-60.

Acrochaetium savianum (Meneghini) Naegeli 1861: 405. Feldmann 1942: 218. Hamel 1927: 41, 98, Fig. 32; 1928: 192; 1928a: 135, Fig. 32. Papenfuss 1945: 311; 1947: 435.

Callithamnion savianum Meneghini 1840: 511. J. Agardh 1851: 14; 1876: 6. Kuetzing 1849: 641.

Chantransia saviana (Meneghini) Ardissonne 1883: 276 (pro parte). DeToni 1897: 68.

Chantransia efflorescens var. *thuretii* Bornet 1904: XVI, pl. 1.

Acrochaetium thuretii (Bornet) Collins et Hervey 1917: 98. Doty 1948: 263. Hamel 1927: 37, 97, Fig. 30. 1928: 191; 1928a: 131, Fig. 30. Kylin 1944: 21, Fig. 14. Papenfuss 1945: 311.

Audouinella thuretii (Bornet) Woelkerling 1971: 36, Figs. 12, 24; 1973: 88.

Chantransia thuretii Bornet. Collins 1900: 49 (nom. nud.).

Chantransia thuretii (Bornet) Kylin 1907: 119, Fig. 28. Rosenvinge 1909: 100, Figs. 30-33.

Rhodochorton thuretii (Bornet) Drew 1928: 171.

Acrochaetium sagraeum auct. non. (Montagne) Bornet: Boergesen 1915: 35 (pro parte). Bornet 1904: XXI (pro parte). Collins 1905: 231 (pro parte); 1906: 192 (pro parte). Collins and Hervey 1917: 97. Collins, Holden, et Setchell 1917: 2181. Hamel 1927: 77, 99 (pro parte); 1928: 173, 191 (pro parte). Hylander 1928: 159 (pro parte) Jao 1936: 244 (pro parte). Papenfuss 1945: 311 (pro parte). Taylor 1937: 233 (pro parte); 1957: 220 (pro parte); 1960: 309 (pro parte).

Chantransia sagraeana auct. non. (Montagne) DeToni: DeToni 1924: 51 (pro parte).

Chantransia virgatula auct. non. (Harvey) Thuret In LeJolis: Collins 1900: 49 (pro parte). Collins, Holden, et Setchell 1895: 39. Hylander 1928: 158.

Plants partly to entirely epiphytic, caespitose, up to 4 mm

tall; original spore non-persistent. Prostrate system composed of short, simple or branched filaments free from one another or united into an irregularly shaped pseudoparenchymateous disc. Erect filaments moderately to freely and irregularly branched. Cells cylindrical, (7-) 8-12 (-14) μm wide and 20-60 μm long [L/D 2-6(-8)] in main axes and laterals, sometimes tapering to 4-6 μm wide near the tips; each cell containing a single parietal lobate chromoplast and one pyrenoid. Unicellular hairs unknown.

Monosporangia ovoid, 10-15 μm wide and 18-27 μm long, sessile or stalked, single or in pairs, in a second series along the laterals or more scattered. Tetrasterangia ovoid, 17-24 μm wide and 26-34 μm long, sessile or stalked, single or in pairs, scattered on the erect filaments.

Other reproductive structures not observed.

Type locality: Genoa, Italy.

Type: FL.

Distribution: Nearly cosmopolitan.

Hosts: A variety of algae and marine angiosperms.

Specimens examined:

MASSACHUSETTS: Sandwich Jetty (Cape Cod Canal), 13. X. 1970, *Woelkerling* (WJW 2818). West Yarmouth, 17. IX. 1969, *Woelkerling* (WJW 2253); 3. X. 1969, *Woelkerling* (WJW 2256). Waquoit Bay (Falmouth), 30. VI. 1969, *Conway* (WJW 1839); 15. IX. 1969, *Conway* (WJW 1840). Woods Hole (Eel Pond), 21. VII. 1970, *Wilce* (WJW 2753). Woods Hole (Nobska) 17. VII. 1970, *Woelkerling* (WJW 2722). Woods Hole, 1876, *Dudley* (WJW 3284).

FRANCE: Cherbourg, 1. IX. 1856, *Bornet* [PC, possibly the type of *Acrochaetium thuretti* (Bornet) Collins et Hervey].

ITALY: Genoa, (8. VI ?). 1839, *Meneghini* (FI, type of *Callithamnion savianum* Meneghini).

Audouinella saviana is distinguished from other New England audouinelloid algae of similar morphology in having a filamentous to pseudoparenchymatous prostrate system without an enlarged panduriform or pyriform cell and having the monosporangia solitary or in pairs on simple stalks rather than in clusters on branched stalks.

Audouinella saviana appears to be confined to the sublittoral and lowermost littoral in New England waters and

has been collected in June, July, September and October as an epiphyte on various algae including *Champia*, *Chondria*, and *Stilophora*. Tetrasporangial plants have been collected in October; sexual plants have not been found in New England waters, but are described in detail by Kylin (1907) and Rosenvinge (1909) [both as *Chantransia thuretii*]. Additional study may reveal that the species is present in New England during all or most of the year.

The vegetative system shows considerable variation in New England populations. In some cases, the prostrate system is quite reduced while in others it is comparatively robust. The L/D ratio of cells also varies considerably. In some plants, most cells are 4-8 diameters long; in others they are mostly 2-4 diameters long; and in still others they show a combination of both of the above (Figs. 57, 59-60).

Acrochaetium thuretii (Bornet) Collins et Hervey is here considered conspecific with *Audouinella saviana* after comparing specimens from the type collections of the two taxa. Material from FI and PC agree in all essential respects with one another and with New England populations (Table 4; also see Addendum).

Plants referable to *Audouinella saviana* appear to be widely distributed, but have usually been reported under the specific epithet "thuretti" while the epithet "saviana" has persisted in relative obscurity. Hamel (1927, 1928a) attempted to distinguish the two taxa on the bases of presence or absence of sexual structures and on the relative L/D ratio of cells, but neither of these criteria appears systematically reliable.

A number of specimens hitherto referred to *Acrochaetium sagraeanum* (Montagne) Bornet have been examined and found to be *Audouinella saviana*; citations have been appended. The type specimen of *Acrochaetium sagraeanum* has been excluded from the Rhodophyta (see "Species Excludendae").

The literature references of Collins (1896, 1906), Collins, Holden, and Setchell (1896), Davis (1913), and Taylor (1937, 1957) to specimens under the names of *Chan-*

transia corymbifera, *C. efflorescens* var. *thuretii*, and/or *Acrochaetium thuretii* are based on misidentifications. These collections have been re-examined and found to contain plants of *Audouinella daviesii*; for further discussion, see the account of that species.

The relationships of *A. saviana* to a number of taxa of similar morphology await clarification. These include *Acrochaetium avrainvillae* Boergesen (1915, p. 48, Figs. 47-49), *A. hypneae* Boergesen (1909), and *A. pallens* (Zanardini) Naegeli (See Hamel 1927, p. 48). All of these taxa appear to be very similar to *Audouinella saviana* and a comparison of type collections may show some or all to be conspecific.

The precise publication date of Meneghini's original diagnosis of *Callithamnion savianum* requires further comment. The issue of *Flora* (Regensburg) containing the diagnosis is dated 28 August 1840; however reference is made on p. 511 of that issue to prior publication of diagnosis on 23 May 1840 in a Pisa "Giornale" (= journal?, newspaper?).

Copies of a three page type-set document dated 23 May 1840 which resemble a journal reprint and are entitled "Lettera del Prof. Giuseppe Meneghini at Dott. Jacob Corinaldi a Pisa" are located at FI and PC (Dr. Paul Silva, personal communication); Prof. Peter S. Dixon has kindly sent me a photocopy of the PC document. Hamel (1927, 1928) also has made reference to this document. The PC copy unfortunately provides no clues as to the original place of publication other than three words — "Pisa Tipografia Prosperi" — written in longhand at the bottom of the first page, and until further light can be shed on the matter of its original place of publication (if, indeed, there was one), it seems wise to continue to refer to the "Flora" article when citing Meneghini's original diagnosis of *Callithamnion savianum* since the wording of the diagnosis in "Flora" is identical to that in the PC document.

7. ***Audouinella unifila*** (Jao) comb. nov. Figs. 44-45.

Acrochaetium unifilum Jao 1936: 239, pl. 10, Figs. 26-32.

Taylor 1937: 228, pl. 32, Figs. 26-32. Non. *A. unifilum* Levring 1953: 472, Fig. 9 (= *Colaconema nakamurai* Woelkerling 1971: 46, Fig. 16).

Chromastrum unifilum (Jao) Papenfuss 1945: 322.

Kylinia unifila (Jao) Papenfuss 1947: 437. Taylor 1957: 212, pl. 32, Figs. 26-32.

Audouinella australis (Levring) Woelkerling 1971: 25, Figs. 4-5.

Kylinia australis Levring 1953: 487, Figs. 21A-C. Boney and White 1967: 595.

Plants epiphytic, up to 150 μm tall; original spore persisting as a hemispherical unicellular base appressed to the substrate and usually giving rise to a single erect filament. Erect filament(s) procumbent to semi-upright, simple or rarely with 1-2 celled laterals. Cells cylindrical, 6-8 μm wide and 8-20 μm long, L/D 1-3, each cell containing a single parietal lobate to stellate (Jao 1936) chromoplast and one pyrenoid. Terminal and pseudolateral hairs up to 50 μm long occur.

Monosporangia ovoid, 5-7 μm wide and 8-14 μm long, sessile or occasionally on unicellular stalks, scattered along the erect filament(s).

Other reproductive structures not observed in New England populations.

Type Locality: Norton Point, Martha's Vineyard, Massachusetts.

Type: MICH, Woods Hole No. 274.

Distribution: Massachusetts; South Australia.

Hosts: *Arthrocladia villosa* Duby, *Audouinella* sp.

Specimens examined:

MASSACHUSETTS: Norton Point (Martha's Vineyard), 3. VIII. 1934, Jao (Michigan, holotype).

AUSTRALIA: Pennington Bay (Kangaroo Island), 7. II. 1947, Womersley (ADU, A31373, isotype of *Kylinia australis* Levring). Note: Other Australian collections examined are cited in an earlier paper (Woelkerling, 1971, p. 26).

Audouinella unifila is distinguished from other New England audouinelloid algae with a unicellular base by

the procumbent development of erect filaments and the characteristically flattened (compressed) hemispherical basal cell.

The one known New England collection of this taxon is the type collection, plants of which are on the permanent slides in MICH. Only monosporangial specimens occur, and the range of cell and spore dimensions of these plants is somewhat greater than reported originally by Jao (1936). Chromoplasts were not recognizable, but at least one pyrenoid was observed.

Critical comparisons of the type collections of *A. unifila* and *A. australis* strongly indicate that the two taxa are conspecific. Monosporangial plants of both taxa show virtually identical ranges of cell and spore dimensions and in general have the same habit. Apparent differences in chromoplast shape (Jao, 1936, reported stellate plastids in *A. unifila*; Levring (1953) recorded parietal plastids in *A. australis*) do not appear to be taxonomically significant (see Woelkerling 1971, p. 14). Woelkerling (1971, p. 26) previously noted similarities in the two taxa.

Although sexual plants do not occur in the type collection, this taxon is referred to *Audouinella* on the basis of the rather common occurrence of sexual plants in South Australian populations.

Some questions may be raised as to the relationships between *Audouinella unifila* and *A. microcopica*. The author's experience to date indicates that the two have quite distinct basal cells and modes of erect filament development, and no intermediates have been observed. However, the possibility exists that such intermediates do occur and they should be watched for.

COLACONEMA Batters

Colaconema Batters 1896: 8. Woelkerling 1971: 40. Non *Colaconema* Schmitz In Schmitz and Falkenberg 1897: 452.

Note: Species not referable to *Colaconema* have been placed in the past in *Acrochaetium*, *Audouinella*, *Calli-*

thamnion, *Ceramium*, *Chantransia*, *Chromastrum*, *Kylinia*, *Rhodochorton*, and/or *Trentepohlia*.

Plants epibiotic, endobiotic, or saxicolous; attached to or suspended in the substrate by a single-celled holdfast or more commonly by a prostrate system of simple or branched filaments, which may or may not become pseudoparenchymatous. Erect filaments, when present, simple or branched, up to 10 mm tall; cells containing one to a number of variously shaped chromoplasts with or without pyrenoids.

Asexual reproduction by sessile or stalked monosporangia, bisporangia, tetrasporangia, and/or multipartite sporangia borne on the erect and/or prostrate filaments.

Sexual reproduction unknown.

Type Species: Colaconema bonnemaisoniae Batters.

Section I

The species in this section are not known to contain pyrenoids in their chromoplasts.

8. ***Colaconema membranacea*** (Magnus) comb. nov. Figs. 64-65.

Audouinella membranacea (Magnus) Papenfuss 1945: 326; 1947: 438. Edelstein and McLachlan 1966a: 1052. Taylor 1957: 224, pl. 31, Figs. 11-12.

Callithamnion membranaceum Magnus 1874: 67, tab. II. Figs. 7-15. Collins 1883: 56; 1888: 10.

Rhodochorton membranaceum (Magnus) Hauck 1885: 69 (only as to binomial). Collins 1894: 230; 1900: 51, 1911: 280. Collins, Holden and Setchell 1895a: 99. Davis 1913: 818. DeToni 1903: 1513. Drew 1928: 186. Hamel 1927: 59, 109, Fig. 39A-E; 1928: 202; 1928a: 152, Fig. 39A-E. Hauck and Richter 1888: 154. Hylander 1928: 169. Kuckuck 1897: 337 et seq., Figs. 1-7. Taylor 1937: 240, pl. 31, Figs. 11-12.

Plants endozoic; original spore non-persistent. Prostrate system consisting of irregularly branched filaments of

indefinite length which may be free from one another or pseudoparenchymatously united into a sheet-like endozoic thallus. Cells of prostrate filaments cylindrical to irregular in shape, 8-60 μm long, and 5-11 μm wide, L/D 0.75-5(-8); each cell containing several to many discoid or irregularly shaped chromoplasts (sometimes becoming more or less spirally twisted) without pyrenoids. Erect filaments, when present, simple or sparingly and irregularly branched, rarely more than 25 cells long. Cells 10-45 μm long and 7-13 μm wide, L/D 1-4.

Tetrasporangia ovoid to globose, 10-15 μm wide and 16-25 μm long, solitary, sessile or occasionally stalked, terminal or rarely lateral on erect filaments or on prostrate filaments.

Type locality: Store Baelt Channel, between Sporogoe Island and Korsøer, Denmark.

Type: ?

Distribution: Europe and cooler waters of both coasts of North America.

Hosts: A variety of marine invertebrates, especially hydroids.

Specimens examined:

CONNECTICUT: Charles Island (Milford Channel), 22. IV. 1889, *Holden* (NY).

MAINE: Eagle Island, VII. 1894, *Collins* (NY).

MASSACHUSETTS: Brandt Point (Marshfield), 7. IV. 1968, *Greenwich* (NHA). Gay Head (Martha's Vineyard), 3. VIII. 1948, *Doty* (U. Hawaii). Marblehead, 30. V. 1884, *Collins* (NY). Martha's Vineyard, 16. VII. 1941, *Taylor* (FH). Nahant, 14. V. 1882. *Collins* (NY); 1. V. 1970, *Woelkerling* (WJW 2545). Revere Beach (Boston), IV. 1885, *Collins* (NY); 29. V. 1886, *Collins* (NY, FH = Hauck and Richter 1888, No. 154); 10. VI. 1894, *Collins* (NY). Sandwich Jetty (Cape Cod Canal), 13. X. 1970, *Woelkerling* (WJW 2812). Sconset Beach, 13. VIII. 1886, *Collins* (NY). Scusset Beach, 29. III. 1969, *LaPlante* (UNH). Woods Hole, 7. IV. 1968, *Logan* (NHA); 6. IV. 1968, *Kastelowitz* (NHA).

NEW HAMPSHIRE: Cedar Point (Dover), 21. XII. 1966, *Hehre* and *Conway* (NHA); 3. III. 1967 *Hehre* (NHA). Hilton Park (Dover Point), 19. III. 1967, *Hehre* and *Conway* (NHA); 27. IV. 1967, *Hehre* and *Stone* (NHA). Rye Ledge, 5. II. 1970, *Woelkerling* (WJW 2336).

NEW YORK: Montauk Point (Long Island), 20. I. 1970, *Woelkerling* (WJW 2258).

Colaconema membranacea is distinguished from other New England audouinelloid algae in having several to many irregular to discoid to spiral chromoplasts without pyrenoids and in having solitary tetrasporangia that are borne in a sessile condition or on simple stalks rather than in clusters on branched gonimoblast filaments. In addition, this species is known to occur only as an endozoophyte in hydroids and several other types of invertebrates, and while this in itself is no criterion of specific distinction, it can serve as a useful ecological guide for identification purposes.

Colaconema membranacea has been collected throughout the year in New England waters and commonly occurs on hydroids in both the intertidal zone (especially hydroids attached to *Ascophyllum* or *Fucus* in shaded habitats) and the sublittoral zone. Often the hydroids become reddish as a result of the algal infestation.

Among New England populations, the nature of the vegetative system varies considerably. In lightly infested host animals, the prostrate filaments tend to remain largely free from one another, but under more crowded conditions, the prostrate system becomes pseudoparenchymatous and all traces of a filamentous character are lost (Fig. 64). In most populations the erect system is entirely suppressed and sporangia, when present, are borne directly on the prostrate filaments. In a few instances, however, the erect systems were more highly developed and consisted of branched filaments up to 750 μm long.

The nature of the life cycle of this species awaits clarification by means of culture studies, and until such time, it is difficult to suggest definite relationships between *C. membranacea* and other audouinelloid algae. Thus, for example, *Rhodochorton concrescens* (see West 1970a) and *Audouinella purpurea* (see West 1969, 1970) share a number of morphological features with *Colaconema membranacea*, but apparently they have quite different types of life cycles.

The relationships of *C. membranacea* to *Callithamnion entozoicum* Reinsch in Giard (1890) are discussed under the latter species in the section on Species Inquirendae.

Section II

Species in this section have chromoplasts each with only one pyrenoid.

9. **Colaonema humilis** (Rosenvinge) Woelkerling 1971: 44, Figs. 15J-O. Figs. 66-73.

Acrochaetium humile (Rosenvinge) Boergesen 1915: 23. Baardseth 1941: 41. Jorde et Klavestad 1963: 76. Kylin 1944: 22, Fig. 17. Levring 1953: 478. Schiffner 1931: 143. Sundene 1953: 185.

Chantransia humilis Rosenvinge 1909: 117, Figs. 44, 45. Boergesen 1927: 21. Levring 1935: 37, Figs. 7F-S; 1937: 89; 1940: 78, Figs. 23A-B; 1942: 8.

Chromastrum humile (Rosenvinge) Papenfuss 1945: 323.

Kylinia humile (Rosenvinge) Papenfuss 1947: 437.

Rhodochorton humile (Rosenvinge) Drew 1928: 151, 169.

Acrochaetium radiatum Jao 1936: 246, pl. 10, Figs. 18-25. Edelstein et al. 1967: 196. Papenfuss 1945: 310. South and Cardinal 1970: 2079. Taylor 1937: 237, pl. 32, Figs. 18-25; 1957: 223, pl. 32, Figs. 18-25.

Plants epiphytic, up to 60 μm tall exclusive of hairs; developing from septate or occasionally aseptate spores. Prostrate system consisting of 2-6 simple or sparsely branched filaments up to 300 μm long, arising from the spore and creeping or forming an irregular, more or less pseudoparenchymatous disc. Cells of prostrate filaments cylindrical or occasionally somewhat subglobose, 6-14 μm long and 4-8 μm wide, L/D 1-2; each cell containing a single chromoplast and one pyrenoid. Erect filaments absent to numerous, simple or sparsely irregularly branched, generally less than 10 cells long; cell dimensions similar

to those of prostrate filaments. Unicellular hairs up to 100 μm long occur.

Monosporangia ovoid, 7-14 μm long and 5-8 μm wide, solitary or occasionally in pairs, sessile or stalked, scattered on prostrate or erect filaments.

Other reproductive structures unknown.

Type locality: Spodobjerg, Langeland, Denmark.

Type: C.

Distribution: Massachusetts; Nova Scotia; Australia; Atlantic and Mediterranean shores of Europe.

Hosts: *Ectocarpus* and *Polysiphonia* in North America; a variety of algae elsewhere.

Specimens examined:

MASSACHUSETTS: Norton Point (Martha's Vineyard), 3. VIII. 1934, *Joa* (MICH, Woods Hole No. 280, type of *Acrochaetium radiatum* Jao). West Falmouth (Harbor), 3. X. 1970, *Woelkerling* (WJW 2767). West Yarmouth, 12. XII. 1969, *Woelkerling* (WJW 2259). Woods Hole (Nobska Point), 26. VI. 1969, *Conway* (WJW 1838); 4. II. 1970, *Woelkerling* (WJW 2329).

NOVA SCOTIA: Ketch Harbor, 31. V. 1965, *Edelstein* (Herb. Nat. Res. Coun., Halifax).

Colaçonema humilis can be distinguished from other New England audouinelloid algae by the following combination of features (as found in the collections examined): 1) A reduced erect system with most filaments of 10 or fewer cells; 2) Cells of erect and prostrate filaments mostly less than two diameters long; and 3) Prostrate system more or less compact; filaments rarely over 500 μm long. The first and third criteria probably do not represent very soundly based systematic characters, but until they can be re-examined in light of additional New England and other collections, they have been offered as useful guides for species recognition in this instance.

C. humilis is known in New England waters from collections made in February, June, August, October, and December. Edelstein et al. (1967) report it from May

through September in Nova Scotia, and judging from this, it seems reasonable to think that it may occur throughout the year in this region.

The erect system varies considerably and may be suppressed altogether (Fig. 67), consist of a few several celled filaments (Figs. 69-70), or of a number of short rather densely crowded filaments (Fig. 73). Likewise the extent of the prostrate system varies according to available substrate space; on the finely filamentous *Ectocapus*, it consists of a very few cells (Fig. 71) but on a larger species of *Polysiphonia* it can spread out more (Fig. 73). Most germinating spores divide into two distinct daughter cells (Fig. 68) but others do not (Fig. 66). Chromoplasts have not been observed; Jao (1936) reports a parietal plastid, Rosenvinge (1909) found a stellate plastid, and Woelkerling (1971) found a variable plastid shape.

Several investigators (e.g. Baardseth 1941, p. 41; Woelkerling 1971, p. 45) have commented upon the possible conspecificity of a number of audouinelloid algae whose morphology is similar to *Colaçonema humilis*. On the basis of the examination of the type and other populations, *Acrochaetium radiatum* Jao has been referred to the synonymy of *Colaçonema humilis*. Jao (1936, p. 247) separated the two taxa on the basis of the former "... having more than two main filaments arising from the divided germinating spore and all the filaments arranged radiately and densely from the center of a fully developed thallus." The type collection of *Acrochaetium radiatum*, however, contains plants that have 2 as well as more than two filaments emanating from the germinating spore (Fig. 68), and has plants that are not densely radiate (Fig. 69) as well as ones that are (see Jao, 1936, pl. 10, Figs. 22-25). Thus the criteria of specific distinction offered by Jao do not appear to be taxonomically reliable, and the two taxa can be considered conspecific.

The relationships of *Colaçonema humilis* to a number of similar taxa (see Baardseth 1941, p. 41 and Woelkerling

1971, p. 45 for names) remains unclear, but there is increasing doubt as to whether many of these are really distinct species. In the Nova Scotia population examined during this study, plants with varying degrees of erect system development occur side by side and agree morphologically with one or several of the taxa cited by Baardseth (1941) and/or Woelkerling (1971). Similar variation occurs among the New England populations. Final clarification must await a comparison of the various type collections (which in many cases represent the only reported collections), but it seems likely that a number of these taxa will eventually be reduced to synonymy.

10. ***Colaconema minima*** (Collins) comb. nov. Figs. 74-76.

Acrochaetium minimum Collins 1908: 133. Collins, Holden, and Setchell 1908: 1493. Davis 1913: 813. Hamel 1927: 89; 1928: 183. Papenfuss 1945: 316. Taylor 1937: 237; 1957: 222.

Chantransia minima (Collins) Collins 1911a: 186. DeToni 1924: 62.

Acrochaetium emergens (Rosenvinge) Weber van Bosse 1921: 194. Hamel 1927: 93; 1928: 186. Jao 1936: 247, pl. 13, Figs. 7, 7B. Papenfuss 1945: 314. Taylor 1937: 235; 1957: 221.

Chantransia emergens Rosenvinge 1909: 128, Fig. 55. DeToni 1924: 67.

Rhodochorton emergens (Rosenvinge) Drew 1928: 151, 188.

Plants epi- to endophytic; sporelings not observed. Prostrate system consisting of irregularly branched filaments of indefinite length creeping on the surface or between the superficial cells of the host. Cells of prostrate filaments cylindrical to irregular in shape, 5-25 (-44) μm long and 3-8 (-14) μm wide, L/D 1-6 (-8); each cell containing a parietal chromoplast and one pyrenoid. Erect filaments 1-5 (-25) cells long, simple or with a few short, irregularly

arranged laterals; cell dimensions similar to those of prostrate filaments.

Unicellular hairs not observed.

Monosporangia ovoid to globose to hemispherical, 5-12 μm long and 4-10 μm wide, solitary or occasionally in pairs, sessile or on 1-2 celled stalks, scattered on the prostrate or erect filaments.

Other reproductive structures unknown.

Type locality: Robinson's Hole, Elizabeth Islands, Massachusetts.

Type: FH.

Distribution: Massachusetts; Denmark; Norway.

Hosts: *Asparagopsis*, *Desmarestia*, *Polysiphonia*.

Specimens examined:

MASSACHUSETTS: Robinson's Hole (Elizabeth Islands), VIII. 1907, Collins (FH, type); (WIS, isotype). [Isotypes have been distributed as No. 1493 in Collins, Holden, and Setchell (1908).] Sandwich Beach (Cape Cod Canal), 30. VI. 1970, Wilce (WJW 2693); 11. VII. 1970, Woelkerling (WJW 2699).

DENMARK: Mollegrund (Hirshals), 8. VIII. 1899, Rosenvinge (C, Algae Marinae Danicae No. 6574, type of *Chantransia emergens* Rosenvinge).

As circumscribed here, *Colaconema minima* can be distinguished from other New England audouinelloid algae by the following combination of features: 1) A prostrate system of indefinite length bearing no or short (1-5 (-25)) celled erect filaments, 2) Sporangia under 15 μm long and 12 μm wide; 3) Cells with single chromoplasts with one pyrenoid each; commonly over two diameters long.

Colaconema minima is known from three Cape Cod, Massachusetts collections. The type and the WIS isotype of the species consist of dried specimens that have proven difficult to work with because of the matted and rather unresponsive (to resoaking and slide making) condition. Nevertheless it has been possible to study and illustrate (Fig. 75) a portion of type material. Cells up to 15 μm long and 7 μm wide and spores up to 11 μm long and

6 μm wide have been found and thus extend the maximum limits recorded for this material by Collins (1908) and Taylor (1937, 1957). Erect filaments of more than 8 cells and cells over 6 diameters long were not encountered.

The two other collections were found growing on *Asparagopsis* and showed over all agreement with the type, although a number of cells were over 15 μm long and sporangia occurred on both prostrate and erect filaments. The relationship of these collections to *Colaçonema americana* Jao is discussed under that taxon, which is regarded here as a "Species Inquirendae."

Critical comparisons of the type collections of *C. minima* and *Chantransia emergens* Rosenvinge (1909, p. 128, Fig. 55) have resulted here in regarding the two taxa as conspecific. They agree in all essential respects (Figs. 74-76; Table 5). Jao (1936, p. 247, pl. 13, Figs. 7, 7B) recorded the latter from New England waters, and Taylor (1937, p. 226; 1957, p. 217) separated it from *Colaçonema minima* on the basis of slight differences in spore width. A comparison of the type collections indicates that this apparent difference is of no taxonomic significance since spores 3-5 μm wide occur in both taxa.

The relationships of *Colaçonema minima* to other auto-uinelloid algae of similar morphology require considerable clarification. *Acrochaetium endophyticum* Batters (1896, p. 386; see also Baardseth 1941, p. 45, Figs. 19E-G) [non *Rhodochorton endophyticum* Kylin 1907, p. 188, Fig. 40 = *Acrochaetium kylinii* Hamel 1927, p. 93; 1928, p. 187 [nec *Liagorophila endophytica* Yamada 1944, p. 16, Fig. 4 (see also Abbott 1966)] appears to have a virtually identical morphology, and when the types can be compared, the two taxa will almost certainly prove to be conspecific, with the specific epithet "endophyticum" having priority. Likewise *Colaçonema americana* Jao and a number of other similar taxa almost certainly will be relegated to conspecificity when critical comparisons of types can be made.

11. *Colaconema secundata* (Lyngbye) Woelkerling 1973: 94, Figs. 7-8. Figs. 77-83.¹

Callithamnion daviesii var. *secundatum* Lyngbye 1819: 129, pl. 41, Figs. β 4-6.

Acrochaetium luxurians (J. Agardh) Naegeli 1861: 405.

Callithamnion luxurians J. Agardh 1851: 14. Hall 1876: 111. Harvey 1853: 242. Jordan 1874: 197; 1874a: 488.

Chantransia luxurians (J. Agardh) Kylin 1907: 117, Fig. 26.

Acrochaetium secundatum (Lyngbye) Naegeli 1861: 405. Collins 1906: 194. Davis 1913: 813; 1913a: 477. South 1970: 1. South and Cardinal 1970: 2079. Taylor 1937: 230, pl. 31, Figs. 1-3.

Callithamnion secundatum (Lyngbye) C. Agardh 1828: 187.

Ceramium secundatum (Lyngbye) C. Agardh 1824: 132.

Chantransia secundata (Lyngbye) Thuret In LeJolis 1863: 106. Collins 1900: 49; 1911: 276. Collins, Holden, and Setchell 1903: 1088. Davis 1913a: 462, 473, 474. Farlow 1875: 376; 1876: 705. Hylander 1928: 158. Kylin 1910: 28.

Chromastrum secundatum (Lyngbye) Papenfuss 1945: 323.

Kylinia secundata (Lyngbye) Papenfuss 1947: 437. Edelstein and McLachlan 1966a: 1052, Fig. 18. Hehre and Mathieson 1970: 206, 237. Mathieson et al. 1969: 132. Taylor 1957: 214, pl. 31, Figs. 1-3.

Acrochaetium subsimplex Levring 1953: 473, Figs.

¹According to the "Programme and Abstracts of the Twenty-first Annual Meeting of the British Phycological Society" (3-5 January 1973), W. J. Borsje, Vrije University, Amsterdam, reported sexual stages of *Acrochaetium virgatulum* in culture. If his plants are the same as New England plants (which, no doubt, will prove to be the case), *Colaconema secundata* (syn. *Acrochaetium virgatulum*) will then be transferred to the genus *Audouinella* as *A. secundata* (Lyngbye) comb. nov. Borsje's abstract also appears in *Br. phycol. J.* 8: 204-5, 1973.

10A-D, 11. Non *Rhodochorton subsimplex* (Harvey) DeToni 1897: 1515.

Acrochaetium tenuissimum (Collins) Papenfuss 1945: 319.

Chantransia tenuissima (Collins) Kylin 1941: 5, Figs. 1e, f.

Colaonema tenuissima (Collins) Woelkerling 1971: 51, Fig. 21.

Rhodochorton tenuissimum (Collins) Drew 1928: 170, pl. 38, Figs. 26, 27.

Acrochaetium virgatulum (Harvey) Bornet 1904: XXII. Collins 1906: 193. Davis 1913: 813; 1913a: 477. Doty 1948: 264. Edelstein et al. 1970: 625. South and Cardinal 1970: 2079. Taylor 1937: 230. Taylor In Lewis 1924: 214.

A. virgatulum f. *luxurians* (J. Agardh) Collins 1906: 194. Collins, Holden, and Setchell 1906: 1393. Hylander 1928: 159. Taylor 1937: 230, pl. 31, Figs. 4-7.

A. virgatulum f. *tenuissimum* (Collins) Collins 1906: 194.

Callithamnion virgatulum Harvey In Hooker 1833: 349. Jordan 1874a: 17.

Chantransia virgatula (Harvey) Thuret In LeJolis 1863: 106. Collins 1880: 162; 1894: 233; 1900: 49; 1911: 276. Davis 1913a: 462, 473, 474. Farlow 1875: 376; 1876: 705. Farlow, Anderson, and Eaton 1881: 157. Grier 1925: 296. Jelliffe 1904: 98. Hylander 1928: 158. Kylin 1910: 28. Rosenvinge 1909: 109, Figs. 37-41.

C. virgatula var. *luxurians* (J. Agardh) Rosenvinge 1909: 110. Collins 1911: 276.

C. virgatula f. *tenuissima* Collins In Collins, Holden, and Setchell 1900: 741.

Chromastrum virgatulum (Harvey) Papenfuss 1945: 323. Doty 1948: 264.

Kylinia virgatula (Harvey) Papenfuss 1947: 437. Hehre and Mathieson 1970: 206, 237. Mathieson et al. 1969: 132. Taylor 1957: 214.

K. virgatula f. *luxurians* (J. Agardh) Collins 1906: 194.

Hehre and Mathieson 1970: 206, 237. Taylor 1957: 214, pl. 31, Figs. 4-7.

Rhodochorton virgatulum (Harvey) Rosenvinge 1935: 7.

Trentepohlia virgatula (Harvey) Farlow 1881: 109, pl. X, Fig. 3. Collins 1888: 312; 1888a: 10. Martindale 1889: 100. Pike 1886: 109.

T. virgatula var. *secundata* (Lyngbye) Farlow 1881: 109. Pike 1886: 109.

Acrochaetium daviesii auct. non. (Dillwyn) Naegeli: Collins 1906: 194 (pro parte?).

Callithamnion daviesii auct. non. (Dillwyn) Lyngbye: Harvey 1853: 243.

Chantransia daviesii auct. non. (Dillwyn) Thuret In LeJolis: Collins 1880: 162 (pro parte?); 1894: 233 (pro parte?); 1900: 49 (pro parte?); 1911: 276 (pro parte?).

Trentepohlia daviesii auct. non. (Dillwyn) Pringsheim: Pringsheim 1862: 26, Taf VIII, Figs. 1-6.

Acrochaetium flexuosum auct. non. Vickers: Collins 1906: 192. Collins, Holden, and Setchell 1910: 1696. Taylor 1937: 233; 1957: 219.

Chantransia flexuosa auct. non. (Vickers) Collins: Collins 1911: 186.

Acrochaetium sagraeanum auct. non. (Montagne) Bornet: Boergesen 1915: 35 (pro parte). Bornet 1904: XXI (pro parte). Collins 1905: 231 (pro parte); 1906: 192 (pro parte). Hamel 1927: 77, 99 (pro parte); 1928: 173, 191 (pro parte). Hylander 1928: 159 (pro parte) Jao 1936: 244 (pro parte). Papenfuss 1945: 311 (pro parte). Taylor 1937: 233 (pro parte); 1957: 220 (pro parte); 1960: 309 (pro parte).

Chantransia sagraeana auct. non. (Montagne) DeToni: 1924: 51 (pro parte).

Plants epiphytic or epizoic, caespitose, up to 3 mm tall; original spore non-persistent. Prostrate system at first forming a small parenchymatous disc usually composed of a central cell and 3-4 peripheral cells; later proliferating in some plants to form a unistratose (rarely a partially bistratose) pseudoparenchymatous disc. Erect filaments sparsely

or moderately to freely and irregularly branched; laterals of variable length and some populations only 1-5 cells long. Cells cylindrical 8-15 (-20) μm wide and 15-100 μm long, L/D (1-) 2-6; each containing an axial or parietal stellate chromoplast and a central pyrenoid. Unicellular hairs up to 300 μm long abundant in some populations,, pseudolateral or terminating 1-3 celled lateral branches; sparse or absent in other populations.

Monosporangia ovoid, 10-20 μm wide and 15-26 (-32) μm long, solitary or in pairs, sessile or stalked, scattered on the erect filaments or sometimes densely crowded on short lateral branches.

Other reproductive structures not observed.

Type locality: Kvivig, Faeroes Islands (on "*Conferva rupestris*").

Holotype: C.

Distribution: Atlantic Coast of North America, Australia, Canary Islands, Europe, Sargasso Sea.

Hosts: A wide variety of algae and on hydroids.

Specimens examined:

CONNECTICUT: Black Rock Beacon (Long Island Sound), 20. VII. 1892, *Holden* (NY, Holden 646) New Haven, prior to 1853, *Hooper* (TCD). Woodmont, 27. VII. 1893, *Holden* (NY).
 MAINE: Eagle Island (Penobscot Bay), 16. VII. 1905, *Collins* (NY). Fox Island, VIII. 1880, *Collins* (NY). Inner Mark Island, 8. VII. 1903, *Collins* (NY, PBA 1088). Kennebec River Mouth, VIII. 1880, *Booth* (NY). Peak's Island, IX. 1874, *Farlow* (FH).
 MASSACHUSETTS: Eastham, 10. VII. 1907, *Collins* (NY). Falmouth (Cape Codder Point), 30. X. 1966, *Conway* et al. (NHA); 19. XI. 1969, *Woelkerling* (WJW 2237); 7. I. 1970, *Conway* (WJW 2294). Falmouth (Monauhan Beach), 12. III. 1969, *Conway* (WJW 1850); (WJW 1851). Falmouth (Waquoit Bay), 21. I. 1969, *Conway* (WJW 1842); 11. III. 1969, *Conway* (WJW 2273); 30. VI. 1969, *Conway* (WJW 2274); 7. VII. 1969, *Conway* (WJW 1845); 15. IX. 1969, *Conway* (WJW 1844); 1. X. 1969, *Conway* (WJW 1841). Gloucester (Niles Beach), IX. 1875, *Farlow* (FH); no date, *Farlow* (NY, Algae Exsic. Am. Bor. — Farlow, Anderson, and Eaton, No. 157). Hingham, prior to 1853, *Brewer* (TCD). Marblehead, 17. VI. 1902, *Collins* (NY). Mattapoisett, 30. V. 1905, *Collins* (NY); 20. X. 1906, *Collins* (NY, PBA 1393). Nantucket (Brauts Point), 16. VIII. 1898, *Collins* (NY). Nantucket (West Jetty, Nant. Center), 14. IV. 1970, *Woelkerling* (WJW 2476). Nantucket (?), prior to 1853, *Durkee* (TCD). New Bedford (Scontient Point),

13. VII. 1927, *Taylor* (NY). Penikese Island, 1. X. 1970, *Woelkerling* (WJW 2808). Sandwich (Cape Cod Canal Jetty), 7. IV. 1968, *Kastelowitz* (NHA); 13. X. 1970, *Woelkerling* (WJW 2816). West Falmouth (Harbor entrance), 10. XII. 1969, *Conway* (WJW 2131); 6. I. 1970, *Woelkerling* (WJW 2276). Woods Hole, VII. 1875, *Farlow* (FH); VII. 1903, *Collins* (NY); 10. VIII. 1947, *Abbott* (Abbott 1638); 3. VI. 1966, *Conway* (WJW 2168); 4. II. 1970, *Woelkerling* (WJW 2316); 2. VII. 1970, *Woelkerling* (WJW 2680); 29. I. 1971, *Woelkerling* (WJW 3299); 16. II. 1971, *Woelkerling* (WJW 3315).

NEW HAMPSHIRE: Fort Constitution, 20. IX. 1966, *Conway* and *Hehre* (NHA). Fox Point, 21. VII. 1966, *Conway* and *Shipman* (NHA). Great Boar's Head, 15. X. 1966, *Hehre* and *Conway* (NHA); 11. XII. 1966, *Hehre* and *Conway* (NHA). Little Boar's Head, 14. IX. 1966, *Hehre* (NHA); 25. XI. 1966, *Conway* and *Hehre* (NHA). Rye Ledge, 29. III. 1967 *Mathieson* and *Murphy* (NHA).

NEW JERSEY: Atlantic City, 16. IV. 1892, *Morse* (NY, No. 1696 in the *Phycotheca Boreali Americana*); 1. IX. 1925, *Rose* (NY).

NEW YORK: Cold Spring Harbor, 21. VII. 1893, *Howe* (?) (NY). Little Neck Bay (Long Island), 7. IV. 1966, *Keenan* (NHA).

RHODE ISLAND: Napatree Point, 9-11. X. 1872, *Eaton* (NY); (FH).

CALIFORNIA: San Pedro, XI. 1898, *Monk* (FH, type of *Chantransia virgatula* F. *tenuissima* Collins; ADU A32706, isotype; NY, isotype; WIS, isotype).

EUROPE: England (Torquay), prior to 1833, *Griffiths* (TCD, type of *Acrochaetium virgatulum* (Harvey) Bornet). Faeroes Islands (Kvi-vig), 19. VI. 1817, ? (C, Herb. Lyngbye, type). Sweden (Kattegat Channel), no date, ? (LD 35117, type of *Callithamnion luxurians* J. Agardh).

AUSTRALIA: Musselroe Bay (Tasmania), 7. II. 1948, *Levring* (ADU, A19846, isotype of *Acrochaetium subsimplex* Levring).

Colaconema secundata is distinguishable from other New England audouinelloid algae in 1) having spores germinating to form a distinctive, orbicular parenchymatous group of cells (Fig. 77) which later may proliferate (Figs. 80-81), and in 2) having distinctly stellate chromoplasts (Fig. 83), each with one pyrenoid, in cells of the erect filaments. In addition, most, but not all, New England populations possess a somewhat twiggy (virgate) habit as a result of having numerous 1-3 (-5) celled lateral branches terminated by unicellular hairs (Fig. 82).

Colaconema secundata occurs throughout the year in New England on a variety of algae or invertebrates in the sublittoral, and occasionally appears in the lower littoral,

particularly on *Porphyra*. It probably is found in greater numbers than any other audouinelloid alga in New England waters and most frequently is encountered as a dense fringe on blades of the sea grass *Zostera*.

Rosenvinge (1909) has provided an excellent account of this species (as *Chantransia virgatula*) and of the variation it exhibits; his concept of this species is recognized here (see also Hamel 1927, 1928). As noted previously (Woelkerling 1973, p. 96), the specific epithet "secundata" has nomenclatural priority over the specific epithet "virgatula". The form illustrated in this study (Fig. 82) is by far the most common in New England waters, although individuals of all forms discussed by Rosenvinge (1909) have been observed.

Most previous accounts (e.g. Hamel 1927, Kylin 1907, Rosenvinge 1909) state that the germinating spore divides to form a central cell and three surrounding cells. In all New England plants examined, four cells surround the central cell (Fig. 77); this difference, however, does not appear to be of any taxonomic consequence.

Some variation in the number of cell layers in the basal disc has also been reported. Hamel (1927), Kylin (1907), and Rosenvinge (1909) all record only single layered basal discs. Boergesen (1902) separates *Chantransia secundata* from *C. virgatula* on the basis that the former always has a two layered basal disc while the latter has only a single layered disc. Collins (1906) states that the basal discs are usually two layers thick; Taylor (1937, 1957) follows Boergesen (1902) in recognizing two species in his keys (Taylor 1937, p. 227; 1957, p. 211), but states in his descriptions (Taylor 1937, p. 230; 1957, p. 214) that the base is "... a multicellular disc 1-2 layers or more in thickness"

During this study, several discs (Fig. 80) that are partially two layered have been seen, but the majority are single layered. None of the sort illustrated by Boergesen (1902, p. 350, Fig. 51) or Taylor (1957, pl. 31, Fig. 3) have been encountered. It also appears evident that some

variation can occur in the number of layers in the base within single populations, and therefore, this variation has little taxonomic significance. Indeed, all plants examined in the type collections of *Colaçonema secundata* and the other taxa here considered conspecific have single layered basal discs.

Only monosporangial plants have been observed during the present study; tetrasporangial individuals have, however, been reported in New England by Hehre and Mathieson (1970) and Taylor (1937, 1957). Kylin (1907, 1944) and Rosenvinge (1909), among others, have recorded them from Europe. Sexual stages remain unknown.

Collins in Collins, Holden, and Setchell (1900, No. 741) described and distributed *Chantransia virgatula* f. *tenuissima* based on a collection of Monks from San Pedro, California. Later Drew (1928, p. 170, pl. 38, Figs. 26, 27) raised the taxon to specific rank (as *Rhodochorton tenuissimum* (Collins) Drew), primarily on the bases of somewhat narrower filaments, lack of hairs, and sessile and not opposite sporangia.

The type collection of this species in FH as well as several isotypes (ADU, NY, WIS) have been examined and found to agree well with the types of *Colaçonema secundata* and of *Callithamnion virgatulum*. Type collection plants of all three taxa have the same characteristic development of the basal disc, which in some cases have produced proliferations. The type plants of *Chantransia* f. *virgatula tenuissima* examined also possess (in contrast to what Drew (1928) found in her material) unicellular hairs and do have some stalked monosporangia and some sporangia in an opposite arrangement. In agreement with Drew, most sporangia are sessile and scattered. Drew reported a parietal chromoplast, but this was not evident in the type material examined. Since there appear to be no other reliable criteria of separation, *Chantransia virgatula* f. *tenuissima* and *Colaçonema secundata* are considered here to be conspecific as was suspected earlier (Woelkerling 1971, p. 52).

Acrochaetium subsimplex Levring (1953, p. 473, Figs. 10A-D, 11) likewise is conspecific with *Colaconema secundata* (see Woelkerling 1971, p. 51).

A number of collections referred to *Audouinella daviesii* by Collins (see discussion under that taxon) have been examined and found to contain only (?) plants of *Colaconema secundata*. If one assumes that these collections do not contain a mixture of two taxa (such a mixture was not found during the present study), Collins' material has been misidentified and has been treated accordingly.

Likewise one collection (NY, Holden collection No. 646) hitherto referred to *Acrochaetium sagraeanum* (see Collins 1905, p. 231 and discussion of that taxon under "Species Excludendae") has been found to contain only plants of *Colaconema secundata*; the literature citations have been corrected accordingly.

Two collections in NY (one from Massachusetts and one from New Jersey, the latter being distributed as specimen 1696 in the *Phycotheca Boreali Americana*) hitherto referred to *Acrochaetium* (= *Chantransia*) *flexuosum* by Collins (1906, 1911), Collins, Holden, and Setchell (1910), and Taylor (1937, 1957) have been examined and found to contain only young plants of *Colaconema secundata*. Parenchymatous discs typical of young plants of *C. secundata* are abundant in both collections and in the largest plants these discs have become more or less obscured by subsequent cell division in prostrate system cells. Relatively few sporangia were present, but these fell within the range of dimensions found among other New England populations.

Specimens from Rhode Island referred by Taylor (1937, 1957) to *Acrochaetium flexuosum* have not been available for examination and their status therefore remains in doubt.

OTHER NEW ENGLAND RECORDS

In addition to the species already discussed, several other audouinelloid taxa have been reported from New

England waters. As a result of the present investigation, the occurrence of four of these taxa, discussed below under "Collections Inquirendae", is surrounded by doubt. The taxonomic status of two other taxa, discussed below under "Species Inquirendae", is open to question, and the type collection of a seventh taxon, discussed below under "Species Excludendae", has been referred to the Chlorophyta.

Collections Inquirendae

Acrochaetium attenuatum (Rosenvinge) Hamel 1927: 99; 1928: 192. Edelstein et al. 1970: 625. Jao 1936: 244, pl. 12, Fig. 1. Papenfuss 1945: 308. South 1970: 1. South and Cardinal 1970: 2079. Taylor 1937: 236, pl. 34, Fig. 1; 1957: 222, pl. 34, Fig. 1.

Chantransia attenuata Rosenvinge 1909: 106, Fig. 35. DeToni 1924: 56.

Rhodochorton attenuatum (Rosenvinge) Nakamura 1944: 103, Fig. 3.

For detailed morphological accounts of this taxon, see Nakamura (1944) and Rosenvinge (1909).

Type locality: Jelstrup, Limfjord, Denmark.

Type: C (Rosenvinge 3883).

Distribution: Northern Europe, Eastern Canada, Japan.

Hosts: A variety of algae.

Specimens examined: See below.

This taxon has been recorded once in New England by Jao (1936) from Norton Point, Martha's Vineyard, Massachusetts and subsequently reported by Taylor (1937, 1957). The collection upon which this record is based is apparently represented in MICH by a prepared slide bearing the number Woods Hole 280. (This same slide contains type collection specimens of two other taxa [*Acrochaetium radiatum* Jao and *A. microfilum* Jao] which are regarded here as conspecific with *Colaonema humilis* and *Audouinella microscopia* respectively).

The MICH slide has been examined during this study and found to contain two plants somewhat similar to those

described by Jao (1936), but the material was too fragmentary and too young to make any definite identification, although the specimens showed some features similar to young plants of *Audouinella saviana*. The taxonomic status of these plants therefore remains in doubt as does the occurrence of *A. attenuatum* in New England waters.

Likewise the record of Edelstein *et al.* (1970, p. 265) requires further investigation.

Audouinella efflorescens (J. Agardh) Papenfuss 1945: 326; 1947: 438. Edelstein and McLachlan 1968: 993, Figs. 1-2. Taylor 1957: 225.

Acrochaetium efflorescens (J. Agardh) Naegeli 1861: 405. Hamel 1927: 103; 1928: 196. Taylor 1937: 236.

Callithamnion efflorescens J. Agardh 1851: 15; 1876: 10.

Chantransia efflorescens (J. Agardh) Kjellman 1875: 14; 1883: 129. Kylin 1906: 113, Figs. 1-5; 1907: 119. Rosenvinge 1909: 134, Figs. 61-64.

Grania efflorescens (J. Agardh) Kylin 1944: 26, Fig. 24.

Rhodochorton efflorescens (J. Agardh) Drew 1928: 151. Rosenvinge 1935: 7.

For detailed morphological accounts of this taxon, see Kylin (1906) and Rosenvinge (1909).

Type locality: Kattegat Channel, Sweden.

Type: LD 35129.

Distribution: Arctic, Eastern Canada, Northern Europe.

Hosts: A variety of algae and invertebrates; also on rock.

Specimens examined: Sweden: Kattegat, 13. VIII. 1833, ? (LD 35129, type of *Callithamnion efflorescens* J. Agardh).

This taxon has been recorded (as *Chantransia efflorescens*) on *Rhodymenia* from Gay Head (Martha's Vineyard) Massachusetts by Farlow (1877, p. 245), but neither he nor anyone else apparently has made further reference to this collection. Moreover, no plants of *Audouinella efflorescens* from Gay Head on *Rhodymenia* could be located in FH or NY during this investigation, and this record of

the taxon in New England must therefore remain in doubt.

Farlow (1881, p. 109) also records a *Chantransia efflorescens* Thuret from Gay Head on *Cystoclonium*. Whether this is the same specimen as the one discussed above is uncertain, but plants from the *Cystoclonium* collection, the major portion of which is in FH (a fragment cut from the sheet is in the Collins material in NY), have been examined and found to contain sexual plants of *Audouinella daviesii* rather than specimens of *A. efflorescens*. Carposporophytes of the two are easily distinguishable because carospores are only terminal in *A. daviesii* but occur in rows of 2-3 in *A. efflorescens*. The notes of Taylor (1937, p. 236; 1957, p. 225) refer to Farlow's material on *Cystoclonium*, which is regarded here to belong to *A. daviesii* (q.v. for further comments).

Audouinella efflorescens is a distinctive species with its spirally twisted chromoplasts without pyrenoids and its seriate carospores, and future study may show it to be a component of the New England flora. It apparently has recently been found in Nova Scotia (Edelstein and McLachlan 1968).

Audouinella spetsbergense (Kjellman) comb. nov. Figs. 61-63.

Rhodochorton spetsbergense (Kjellman) Kjellman 1883: 187. DeToni 1903: 1511.

Thamnidium spetsbergense Kjellman 1875: 31, Figs. 11-12.

Rhodochorton penicilliforme (Kjellman) Rosenvinge 1894: 66, Fig. 9; 1923-24: 388, Figs. 325-327. Boergesen 1902: 389, Fig. 60. Collins 1906a: 160. Drew 1928: 176. Edelstein et al. 1967: 200, Figs. 6, 28. Kylin 1907: 188; 1925: 44, Figs. 26a-c; 1944: 28. Taylor 1937: 239; 1957: 225.

Rhodochorton mesocarpum (Carm.) Kjellman var. *penicilliformis* (Kjellman) Kjellman 1883: 187, pl. 16, Figs. 6-7. Rosenvinge 1893: 792.

Thamnidium mesocarpum (Carm.) Kleen f. *penicilliformis* Kjellman 1875: 30; 1877: 25; 1877a: 23.

Plants epiphytic, caespitose, up to 2.0 mm tall; original

spore non-persistent. Prostrate system consisting of an irregularly discoid mass of pseudoparenchymatous filaments. Erect filaments sparingly to moderately and irregularly branched. Cells cylindrical, 8-13 μm wide and (10-) 20-35 (-50) μm long, L/D (1-) 1.5-4 (4.5); each cell containing a number of discoid to irregularly shaped chromoplasts without pyrenoids. Unicellular hairs not observed.

Tetrasporangia ovoid, 25-35 μm long and 16-25 μm wide, single or occasionally in pairs (rarely in groups of 3), sessile or on stalks, scattered over the erect filaments or occasionally terminal on lateral branches.

Other reproductive structures not observed.

Type locality: Fairhavn, Spitzbergen (79° 49' N.).

Type: UPS.

Distribution: In North America, from Washington state northwards on the Pacific coast and Rhode Island northwards (? , see discussion) on the Atlantic Coast; also reported from northern Europe.

Hosts: Various algae and hydroids.

Specimens examined: SPITZBERGEN: Fairhavn Is. (79° 49' N.), 19. VIII. 1872, *Kjellman* (UPS, type). Fairhavn Is. (79° 41' N.), 12. VIII. 1872, *Kjellman* (UPS, type of *R. penicilliforme* (Kjellman) Rosenvinge).

This taxon has been recorded (as *Rhodochorton penicilliforme*) from Rhode Island (Collins 1906a, p. 160) and northern Massachusetts (Taylor 1937, p. 239; 1957, p. 225). Collins material has not been found either in FH or NY and the Massachusetts material has not been available for study. (The taxonomic description given above is based on data gathered from plants in the type collection; see Rosenvinge 1923-24 for a more complete account). Moreover, no additional plants of this taxon have been collected during the present investigation and three collections in NHA examined have been found to contain only plants of other species. Thus, the occurrence of this taxon in New England waters is open to question, and further investigation appears necessary. It has recently been reported from Nova Scotia (Edelstein et al. 1967), but did

not appear in a recent survey of Campobello Island, New Brunswick (Stone et al. 1970).

Kjellman (1875) described two new taxa from collections made on Fairhavn Island, Spitzbergen: *Thamnidium spetsbergense* Kjellman and *T. mesocarpum* (Carmichael) Kjellman forma *pencilliformis* Kjellman. The latter was given species status by Rosenvinge (1894, p. 66). The type specimens of both taxa, preserved on microscope slides in UPS, have been examined during this study and found to be identical in all respects including habit, cell dimensions, spore dimensions, and chromoplast morphology. Consequently, they are here considered conspecific, with the specific epithet "spetsbergense" having nomenclatural priority. It has been referred to the genus *Audouinella* on the basis of Rosenvinge's (1923-24, p. 388, Fig. 27) record of spermatangia. Culture studies may show that *A. spetsbergense* has a diphasic life cycle similar to that of *A. purpurea* (see West. 1969).

The relationships of *A. spetsbergense* and *A. purpurea* require clarification. They differ from one another primarily in their habit (epibiotic vs. primarily saxicolous) and type of prostrate system (pseudo-parenchymatous vs. filamentous) and since none of the characters appear to be taxonomically reliable (see Woelkerling, 1971), the two entities may represent ecological variants of a single species. Because intermediate forms have not been found during this study, they are maintained as distinct taxa for the present.

Colaonema polyides (Rosenvinge) Woelkerling 1971: 49, Figs. 19, 27A.

Acrochaetium polyides (Rosenvinge) Boergesen 1915: 59. Kylin 1944: 26. Papenfuss 1945: 317.

Chantransia polyides Rosenvinge 1909: 132, Figs. 59-60. Levring 1935a: 460, Fig. 2.

For detailed morphological accounts of this taxon, see Rosenvinge (1909) and Woelkerling (1971).

Type locality: Tonneberg Banke, Denmark.

Type: C.

Distribution: Denmark, South Australia, Tasmania.

Hosts: *Codium* (Chlorophyta), *Polyides* (Rhodophyta).

Specimens examined: See below.

This taxon has been reported (as *Acrochaetium polyides*) from New Hampshire (Hehre and Mathieson 1970, p. 205) and Nova Scotia (Edelstein and McLachlan 1966, p. 38, Fig. 2; Edelstein et al. 1970, p. 625; South and Cardinal 1970, p. 2078), apparently in a sterile condition.

The New Hampshire collection and one Nova Scotia collection have been examined; in both cases the meagre amount of sterile Audouinella-like filaments present could not be identified to species with any certainty at all. The taxonomic affinity of these specimens and the occurrence of *A. polyides* in New England and Nova Scotia therefore remains doubtful. It seems likely that these collections have been referred to *A. polyides* solely on the basis of the type of host organism (see Edelstein and McLachlan 1969, p. 555), which, as noted above, is an unreliable criterion of systematic separation.

Species Inquirendae

Colaconema americana Jao 1936: 237, pl. 13, Fig. 8. Levring 1937: 94; 1953: 489. de Valera 1939: 3. Woelkerling 1971: 42.

Acrochaetium americanum (Jao) Papenfuss 1945: 312.

Type locality: Gay Head, Martha's Vineyard, Massachusetts.

Holotype: MICH, Woods Hole No. 272.

Distribution: Type locality; Southern Australia.

Hosts: *Asparagopsis* sp.

The type collection of this species has not been available for examination. Two other collections (WJW 2693, WJW 2699) of *Asparagopsis* containing an endophytic audouineloid alga have been examined and referred to *Colaconema minima* because of overall morphological agreement with that taxon. The cell and spore dimensions of plants in these collections are somewhat smaller than those reported by Jao (1936) for the type collection of *C. americana* (Table

6), and no greatly swollen cells were found, thus placing further doubt (see Woelkerling 1971, p. 42) upon the taxonomic significance of that character. Moreover, the monospores of the collections examined may or may not rest in cup-like bases (Fig. 74), thus casting doubt upon the taxonomic validity of that character also. Upon re-examination, plants in the type collection of *C. americana* will almost certainly be found to be conspecific with *C. minima*.

The rather large number of audouinelloid taxa (including *Colaconema minima* and *C. americana*) whose thallus consists of a creeping prostrate system devoid of or bearing few celled erect filaments present more taxonomic problems and difficulties with identification than any other group within the complex. Such taxa have often been described on the basis of single collections of one or a few plants and have been distinguished on minor differences in cell or spore dimensions, spore arrangement, branching and other morphological characters whose systematic value is dubious (see Woelkerling 1971). Another whole series of such taxa are based on differences in the species of host organism (see Baardseth 1941, p. 46), and host specificity is likewise of doubtful taxonomic value (Woelkerling 1971, p. 11).

Until the type collections of all these audouinelloid algae can be critically compared and the taxa redefined (probably with considerable consolidation of present forms) on firmer morphological grounds, taxonomic procedure dictates a continued recognition of a rather large assemblage of poorly known and rather confusing entities.

Rhodochorton entozoicum (Reinsch In Giard) DeToni 1903: 1514.

Callithamnion entozoicum Reinsch In Giard 1890: 262.

Type locality: Massachusetts.

Type: BM.

Distribution: Apparently known only from the type locality.

Hosts: Marine invertebrates.

The type and only known New England collection of this

taxon has not been available for examination. Reinsch (1879) first described and illustrated material of this taxon from sponges and bryozoans, but as noted by Collins (1883), Reinsch never assigned a name to it. Giard (1890), however, formally described the taxon under the specific epithet of "entozoicum," and this was subsequently recorded by DeToni (1903).

A re-examination of the type collection will almost certainly show that *Rhodochorton entozoicum* is conspecific with *Colaçonema membranaceum*. As noted by Collins (1883), DeToni (1903), and Giard (1890) himself, the two taxa are scarcely distinguishable from one another, and Hamel (1927, p. 59; 1928a, p. 152) regarded the two as conspecific. Hamel, however, gives no indication of having compared the type collections of the two taxa, and the present investigator prefers to defer final judgment until such a comparison can be made. Hamel also regards material of Giard (1890) from Wimeraux as belonging to *C. membranacea*.

Species Excludendae

Acrochaetium sagraeanum (Montagne) Bornet 1904: xxi = *Cladophora sagraena* Montagne 1856: 459.

Bornet (1904) united under the name of *Acrochaetium sagraeanum* specimens from Cuba (Montagne's type, which Bornet noted was sterile), Barbados (see Vickers 1905), California, and Connecticut (see Collins 1905). Later, Collins (1906) and Collins and Hervey (1917) referred specimens from Florida and Bermuda to this taxon.

Montagne's type has been re-examined during this study and found to belong to the Chlorophyta and probably to the genus *Cladophora* itself as originally suggested by Montagne (1856). The specimens have a distinctive green color, lack pit connections and do not possess monosporangia or other reproductive organs, all of which strongly militate against placing Montagne's plants in the *Audouinella* complex as suggested by Bornet.

New England plants referred to *Acrochaetium sagraea-*

num were originally collected by Holden (see Collins 1905, 1906) and are deposited in FH and/or NY. Four of these (Holden collection number 17,701 [= Collins, Holden and Setchell 1895: 39], 708 and 757) contain plants of *Audouinella saviana*. A fifth herbarium sheet (Holden collection number 646) contains plants of *Colaconema secundata*. The sixth collection cited by Collins (1905), Holden 750, could not be located, and its taxonomic status remains in doubt.

Plants in PC from California (which may represent fragments of UC 93071 or UC 789916 deposited at Berkeley) referred by Bornet to *Acrochaetium sagraeanum* have been examined and are referred here to *Audouinella daviesii*. Likewise plants from Barbados (Bornet 1904, Vickers 1905) are referred here to *A. daviesii*. Specimens from Bermuda (Collins and Hervey 1917); Collins, Holden and Setchell 1917, No. 2181), however, belong to *A. saviana*.

Collins (1906, p. 192) cites a collection of *Acrochaetium sagraeanum* from Florida, but no specimens could be located in FH or NY, and its status remains uncertain.

A number of literature references relating to one or more of the above collections can now be clarified. The name *Acrochaetium sagraeanum* (Montagne) Bornet as used by Boergeson (1915, p. 35), Collins (1906, p. 192), Hamel (1927, pp. 77, 99, Fig. 46; 1928, pp. 171, 193, Fig. 46), Jao (1936, p. 244), and Papenfuss (1945, p. 311) refers to the entire assemblage of collections described by Bornet (1904, p. XXI). DeToni (1924, p. 51) employed the name *Chantransia sagraeana* (Montagne) DeToni for Bornet's assemblage. The collection upon which Hamel (1927, 1928) based his illustrations has not been determined.

Vickers (1905, p. 60) relates to the Barbados collection while Collins (1905, p. 231), Collins, Holden and Setchell (1895, No. 39), Hylander (1928, pp. 158, 159), and Taylor (1937, p. 233; 1957, p. 220) pertain to the Connecticut material. The Bermuda collections are cited in Collins and Hervey (1917, p. 97) and Collins, Holden and Setchell (1917, No. 2181), Taylor (1960, p. 309) includes both the

Bermuda and Barbados collections. Corrected citations for these literature references have been listed under the synonymy of *Audouinella daviesii*, *A. saviana*, and *Colaconema secundata*.

EASTERN CANADIAN AND ARCTIC RECORDS

According to South and Cardinal (1970), 28 species of audouinelloid algae have been recorded from the eastern Canadian coast from Cape Chidley, Labrador southwards to the New Brunswick-Maine border.

In addition to those taxa listed from eastern Canada and the Arctic in the descriptive catalogues of Taylor (1937, 1957), seven other taxa have been reported in this region, chiefly as a result of the Nova Scotia studies of Edelstein and McLachlan (1966, 1968, 1969) and of Edelstein et al. (1967, 1970). These include *Acrochaetium bornetii* Papenfuss, *A. endozoicum* (Darbishire) Batters, *A. inclusum* (Levring) Papenfuss, *A. kylinii* Hamel, *A. ralfsiae* Boergesen, *A. subtilissimum* (Kuetzing) Hamel, and *Kylinia cytophaga* (Rosenvinge) Kylin.

A number of these records appear highly questionable. Thus, for example, Edelstein and McLachlan (1969, p. 558) record *Acrochaetium kylinii*, *A. ralfsiae*, and *A. subtilissimum* from Nova Scotia (the only records for this region) on the basis of some endophytic portions of sterile specimens with the comment ". . . we regard these species as preliminary records only." Other records of similar merit also occur (e.g. the Canadian record for *A. polyides* [Edelstein and McLachlan 1966, p. 38] apparently is based on sterile material), and in other cases taxa have been identified on the basis of type of host organism (Edelstein and McLachlan 1969, p. 555) or similar criteria which are of dubious taxonomic significance.

Until all of the specimens involved in publication records for the Cape Chidley, Labrador to New Brunswick-Maine border region can be critically re-examined along with other available material from the area (a task beyond the

scope of the present paper), the number and distribution of audouinelloid algae along these coasts must necessarily remain uncertain. South and Cardinal (1970, p. 2079, footnote 3) also state that many of the species require further investigation.

Only scattered records of audouinelloid algae north of Cape Chidley, Labrador have appeared in the literature and most of these are summarized in the papers of Kjellman (1883) and Lund (1959) and the catalogues of Taylor (1937, 1957). Until relevant herbarium specimens and additional field collections become available for study, the nature and distribution of audouinelloid algae in arctic regions will likewise remain uncertain.

SUMMARY

The systematics, morphology, ecology, and distribution of marine representatives of the *Audouinella* complex (Acrochaetiaceae, Rhodophyta) in New England waters (including New York and New Jersey) have been studied. These investigations support the taxonomic proposals of Woelkerling (1971) and have resulted in the recognition of two genera and eleven species to occur definitely in this region. Seven species, known to reproduce sexually are referred to *Audouinella*; the form genus *Colaconema* contains four New England representatives which are unknown in the sexual state.

A number of published records based on misidentifications have been corrected and in one instance, the type specimen of a taxon [*Acrochaetium sagraeanum* (Montague) Bornet] has been excluded from the Rhodophyta. Records of questionable occurrence, taxa whose status is in doubt, and the state of knowledge of marine audouinelloid algae in eastern Canada and the Arctic are considered briefly.

ACKNOWLEDGMENTS

Sincere thanks are due the curators of the algal collec-

tions housed at the following institutions for the loaning of relevant herbarium specimens: Atlantic Regional Laboratory, Halifax, Nova Scotia; the Botanical Museum and Herbarium, Copenhagen; the Botanical Museum, Lund; the Farlow Herbarium, Harvard University; the Herbarium Universitatis Florentinae, Firenze, Italy; the Institute of Systematic Botany, University of Uppsala; the National Museum of Canada; the National Museum of Wales, Cardiff, U.K.; the New York Botanical Gardens; the Museum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris; the Rijksherbarium, Leiden, Netherlands; Rutgers University; Trinity College, Dublin, Ireland; the University of Adelaide; the University of California; the University of Hawaii; the University of Michigan; and the University of New Hampshire.

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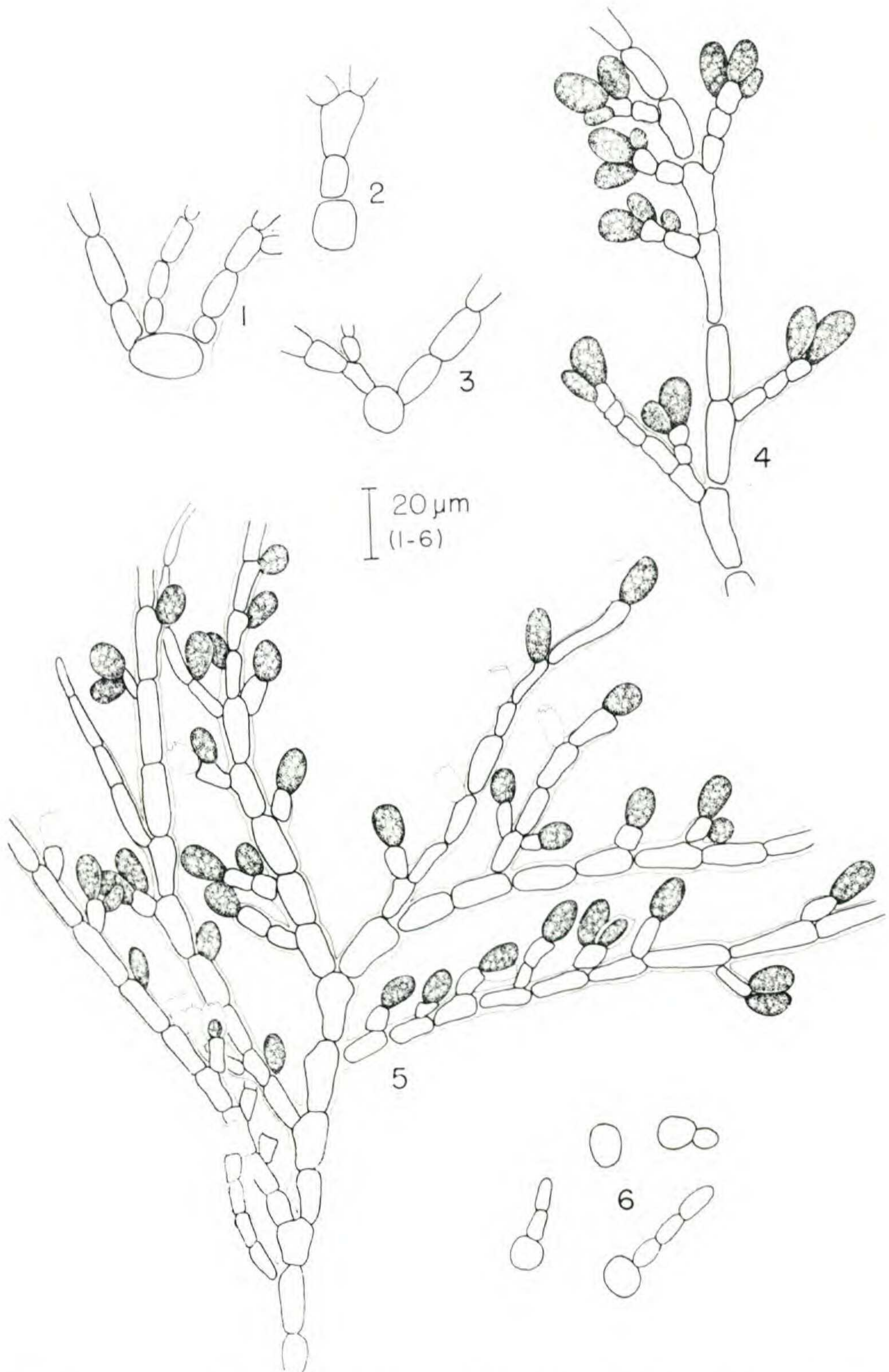
ADDENDUM

After this article had gone to press, Professor Peter S. Dixon provided me (personal communication) with some additional information about the typification of *Audouinella daviesii* and *A. thuretii*.

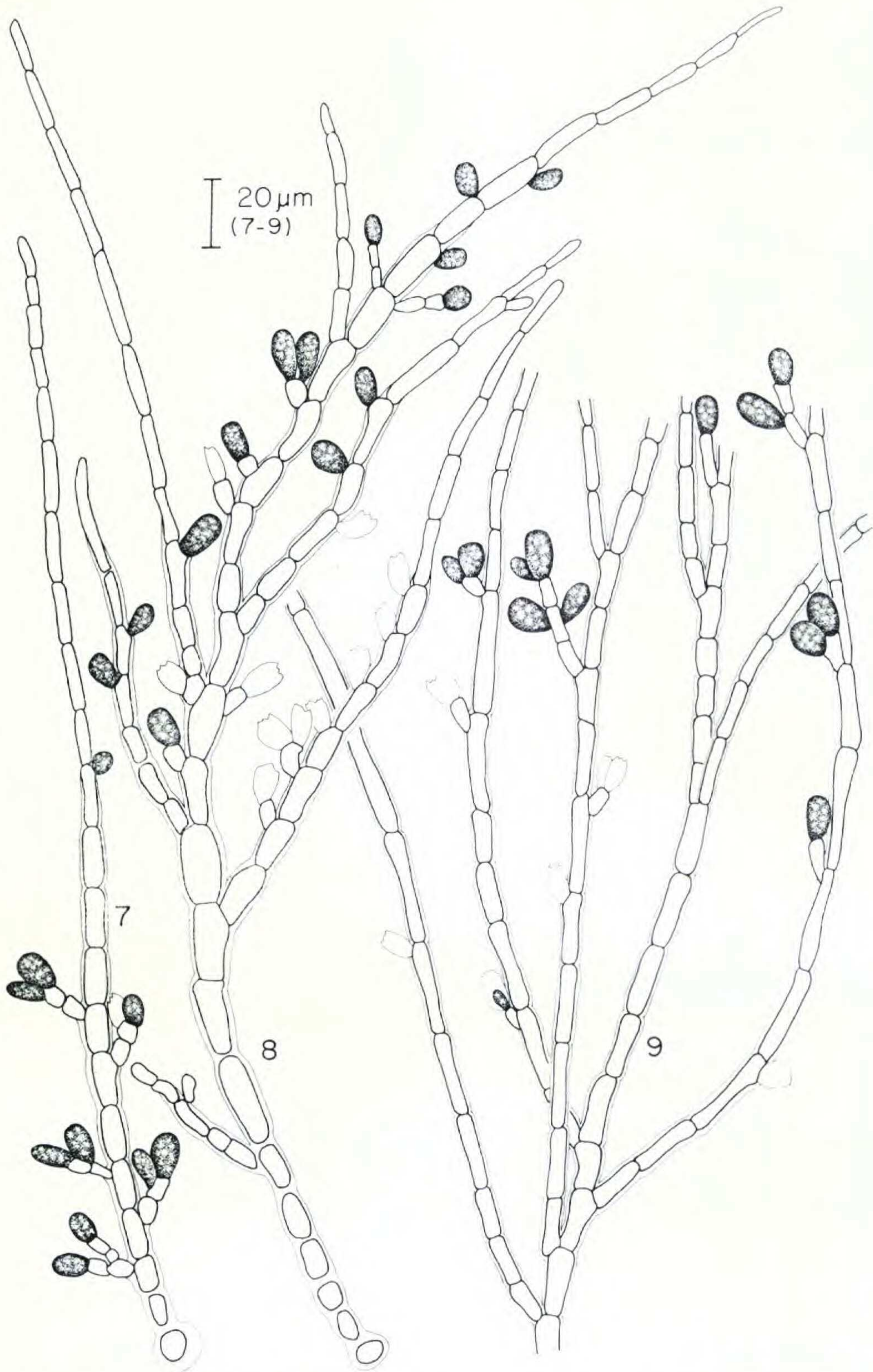
According to Professor Dixon, the only specimen of *Conferva daviesii* in the Dillwyn collections at NMW comes from Swansea rather than from Bantry Bay, the type locality given by Dillwyn. A fragment of the NMW collection was sent to me on loan, and an examination of it indicated that it was material of *C. daviesii*. However, since this specimen apparently does not come from Bantry Bay, it

can at best be regarded only as authentic material rather than type material and the statements in the body of this paper should be modified accordingly.

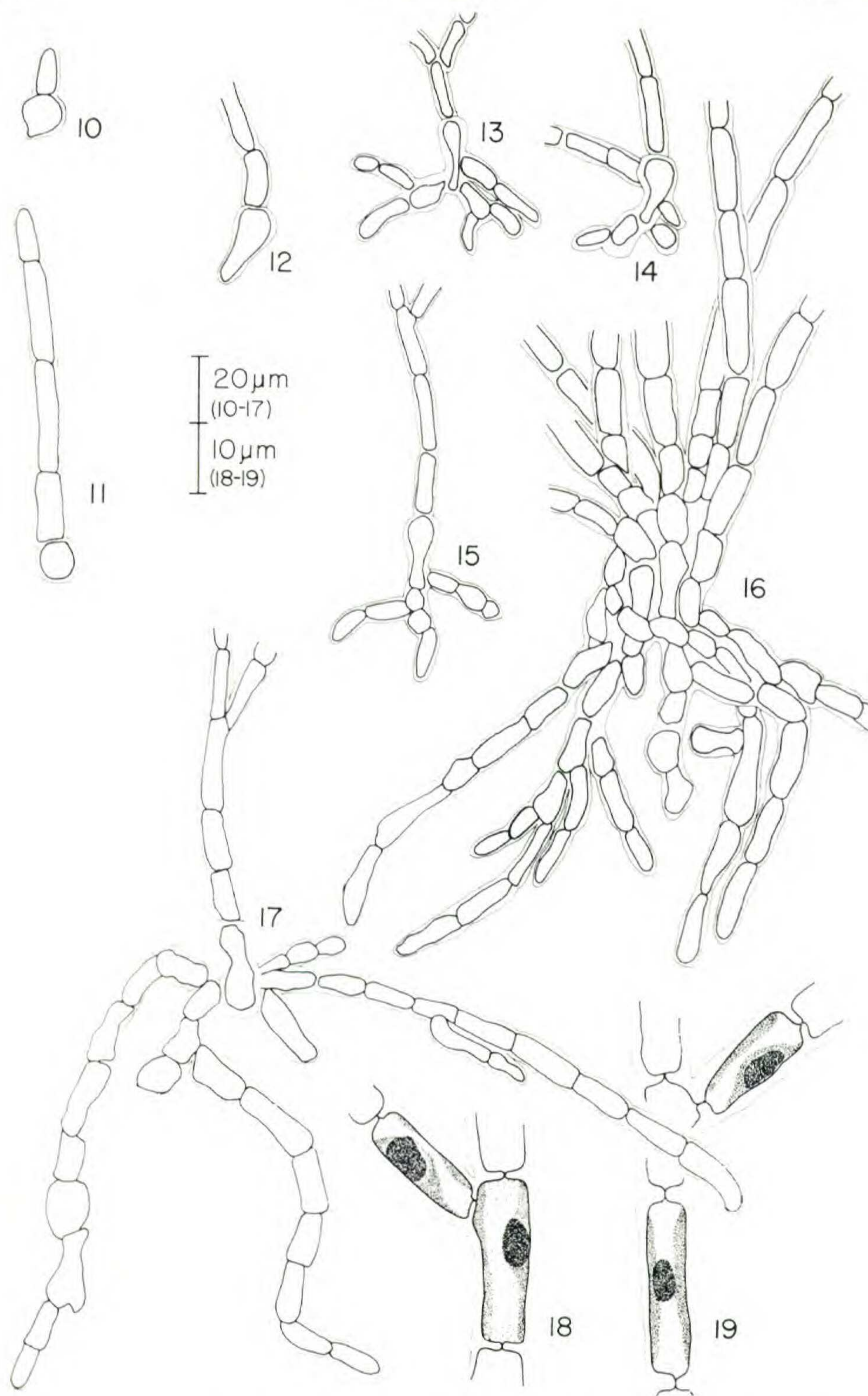
Professor Dixon also informed me that the type material of *Audouinella thuretii* should be dated 5. IX. 1853 (see Bornet 1904), but that the earliest material he could find in PC is dated 1. IX. 1856. Portions of the latter collection have been examined during this study. Until the matter of the dates is further clarified, the 1856 material should be regarded as authentic rather than type, and statements in the body of this paper should be modified accordingly.



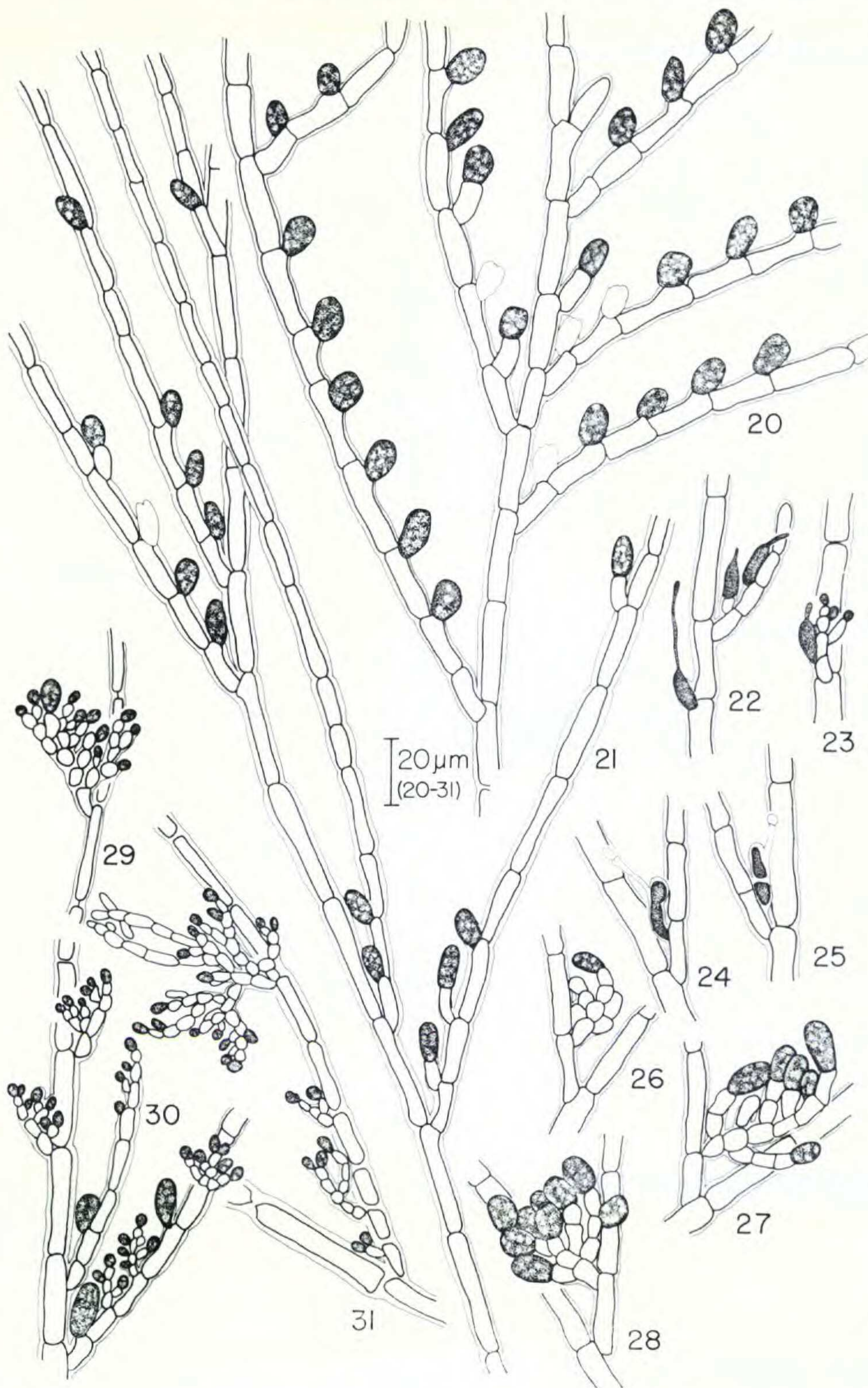
Figs. 1-6. *Audouinella alariae* (Jonsson) Woelk. Figs. 1-3. Unicellular bases bearing a variable number of erect filaments. Figs. 4-5. Portions of densely branched erect filaments with numerous **mono**-sporangia. Fig. 6. Sporelings. Figs. 1 3, 4: NY (Hardhead Island, Penobscot Bay, Maine, VII. 1894, *Collins* [= Collins, Holden, and Setchell 1896a: 236]); Fig. 2: NY (Hampton, New Hampshire, VII. 1894, *Collins*); Fig. 5: WJW 2275 (Nubble Light, Maine, 19. VIII. 1969, *Hehre*); Fig. 6: FH (Casco Bay, Maine, VII. 1939, *Weatherill*).



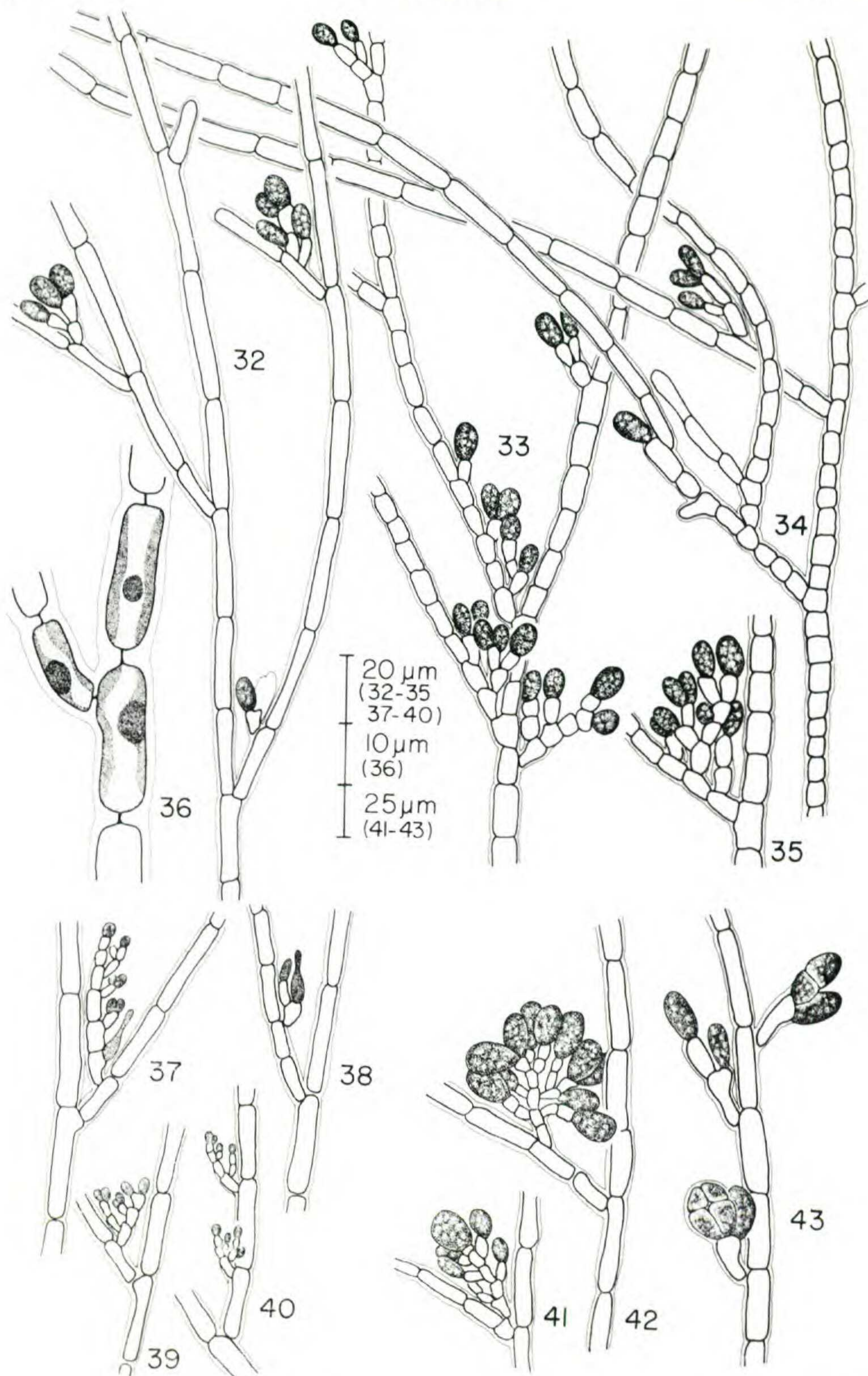
Figs. 7-9. *Audouinella alariae* (Jonsson) Woelk. Figs. 7-8. Habits of fairly small plants with mature monosporangia. Fig. 9. Portion of sparsely branched erect system with scattered monosporangia. Fig. 7: NY (Hardhead Island, Penobscot Bay, Maine, VII. 1894, Collins [= Collins, Holden, and Setchell 1896a: 236]); Figs. 8, 9: WJW 2275 (Nubble Light, Maine, 19. VIII. 1969, Hehre).



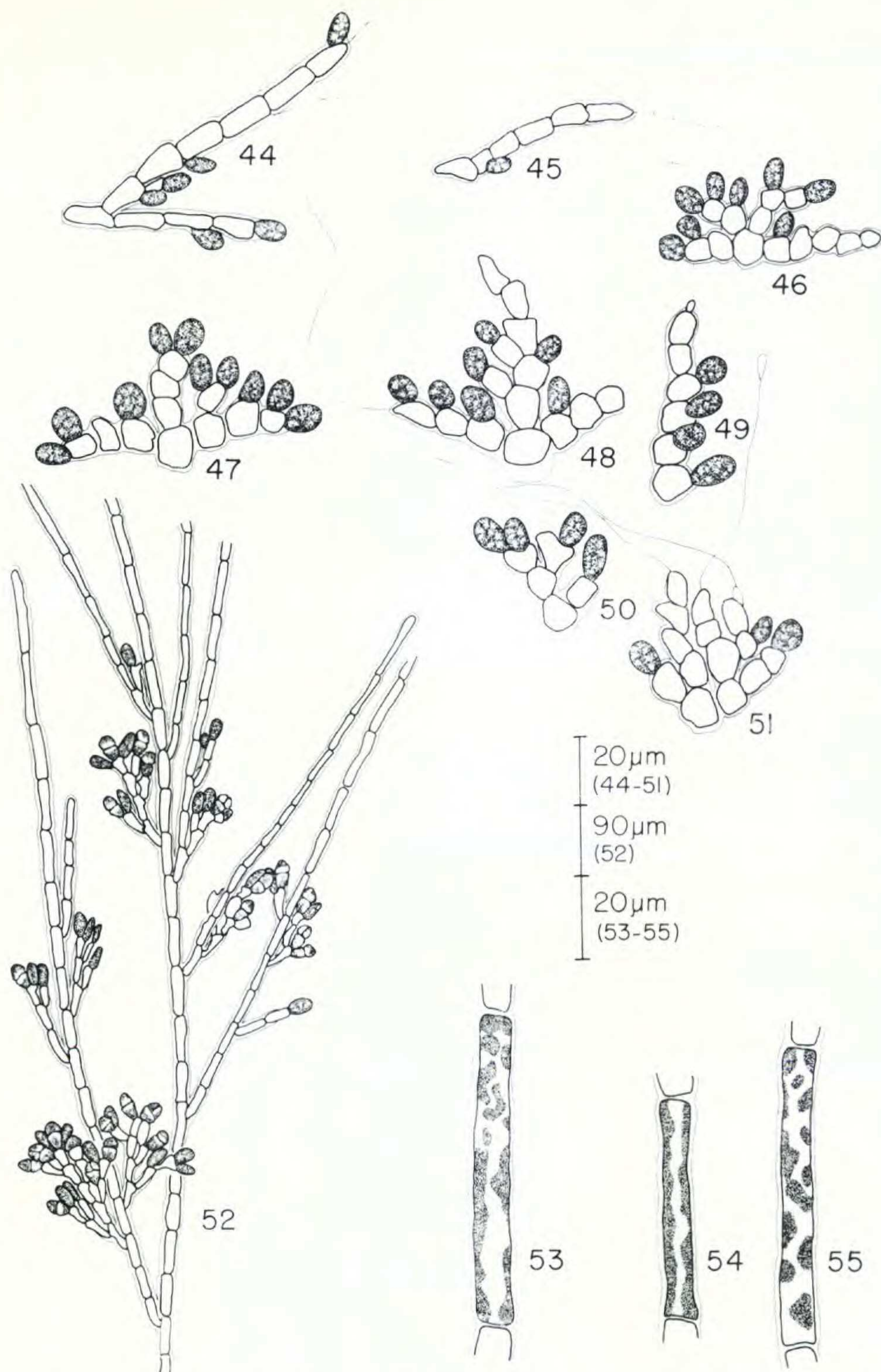
Figs. 10-19. *Audouinella dasyae* (Collins) Woelk. Figs. 10-12. Sporelings. Figs. 14-17. Variation in structure of prostrate system. Note central panduriform to pyriform cell which may become obscured in robust specimens (Fig. 16). Figs. 18-19. Chromoplasts in cells of erect filaments. Figs. 10-12: wjw 2853 (Old Silver Beach, West Falmouth, Massachusetts, 31. X. 1970, *Woelkerling*); Figs. 13, 14: Edelstein 2563 (Malpeque Bay, Prince Edward Island, 5. VIII. 1966, *Edelstein*); Figs. 15, 18, 19: wjw 3311 (Woods Hole, Massachusetts, 16. II. 1971, *Woelkerling*); Fig. 16: wjw 2977 (Old Silver Beach, West Falmouth, Massachusetts, 30. XII. 1970, *Woelkerling*); Fig. 17: wjw 2534 (Waquoit Bay [Harbor Entrance], Falmouth, Massachusetts, 27. IV. 1970, *Woelkerling*).



Figs. 20-31. *Audouinella dasyae* (Collins) Woelk. Figs. 20-21. Filaments of erect system with monosporangia. Figs. 22-23. Unfertilized carpogonia. Figs. 24-25. Fertilized carpogonia. Note transverse division (Fig. 25). Figs. 26-28. Stages in development of carposporophyte. Figs. 29-31. Spermatangia. Note varying arrangement. Fig. 20: wjw 3311 (Woods Hole, Massachusetts, 16. II. 1971, *Woelkerling*); Fig. 21: wjw 2820 (Woods Hole, Massachusetts, 13. X. 1970, *Woelkerling*); Figs. 22-23: FH (North Eastham, Massachusetts, 9. VIII. 1959, *Lamb* A-174 [filed under the host, *Dasya pedicellata*]); Figs. 24-28, 30: wjw 1852 (West Yarmouth, Massachusetts, 3. X. 1969, *Woelkerling*); Figs. 29, 31: wjw 2249 (West Yarmouth, Massachusetts, 16. XI. 1969, *Woelkerling*).



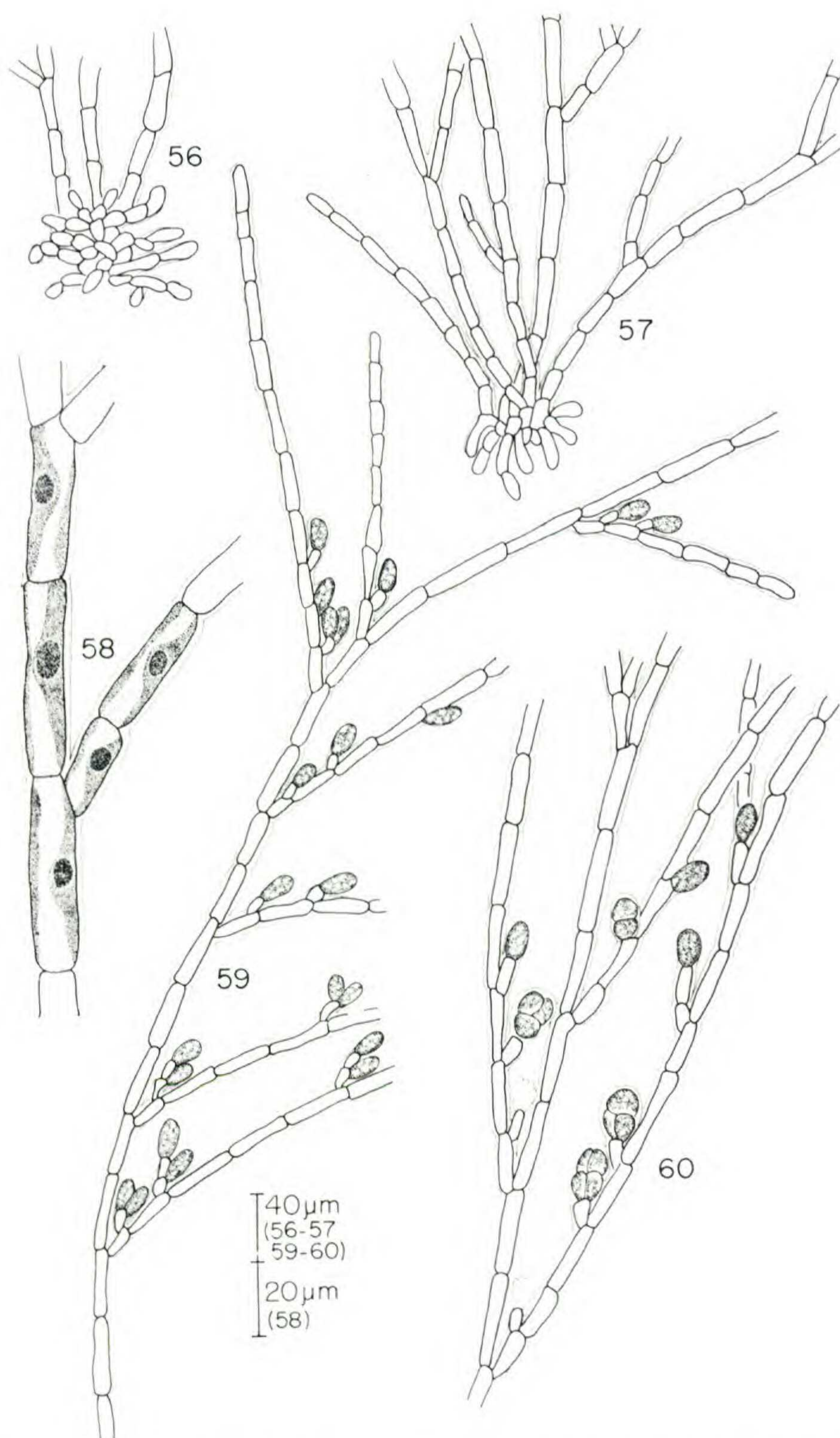
Figs. 32-43. *Audouinella daviesii* (Dillwyn) Woelk. Figs. 32-35. Filaments of erect system bearing monosporangia. Note clustered arrangement of sporangia and variation in cell size. Fig. 36. Chromoplasts in cells of erect filaments. Figs. 37-40. Spermatangia and unfertilized carpogonia. Figs. 41-42. Stages in carposporophyte development. Fig. 43. Tetrasporangia. Fig. 32: wjw 2719 (Woods Hole, Massachusetts, 17. VII. 1970, *Woelkerling*); Fig. 33: wjw 2978 (Old Silver Beach, West Falmouth, Massachusetts, 30. XII. 1970, *Woelkerling*); Fig. 34: wjw 2536 (Waquoit Harbor, Falmouth, Massachusetts, 27. IV. 1970, *Woelkerling*); Fig. 35: wjw 3302 (Woods Hole, Massachusetts, 29. I. 1971, *Woelkerling*); Fig. 36: wjw 2332 (Woods Hole, Massachusetts, 4. II. 1970, *Woelkerling*); Figs. 37-42: wjw 2678 (Woods Hole, Massachusetts, 2. VII. 1970, *Woelkerling*); Fig. 43: wjw 2198 (Montauk Point, New York, 20. I. 1970, *Woelkerling*).



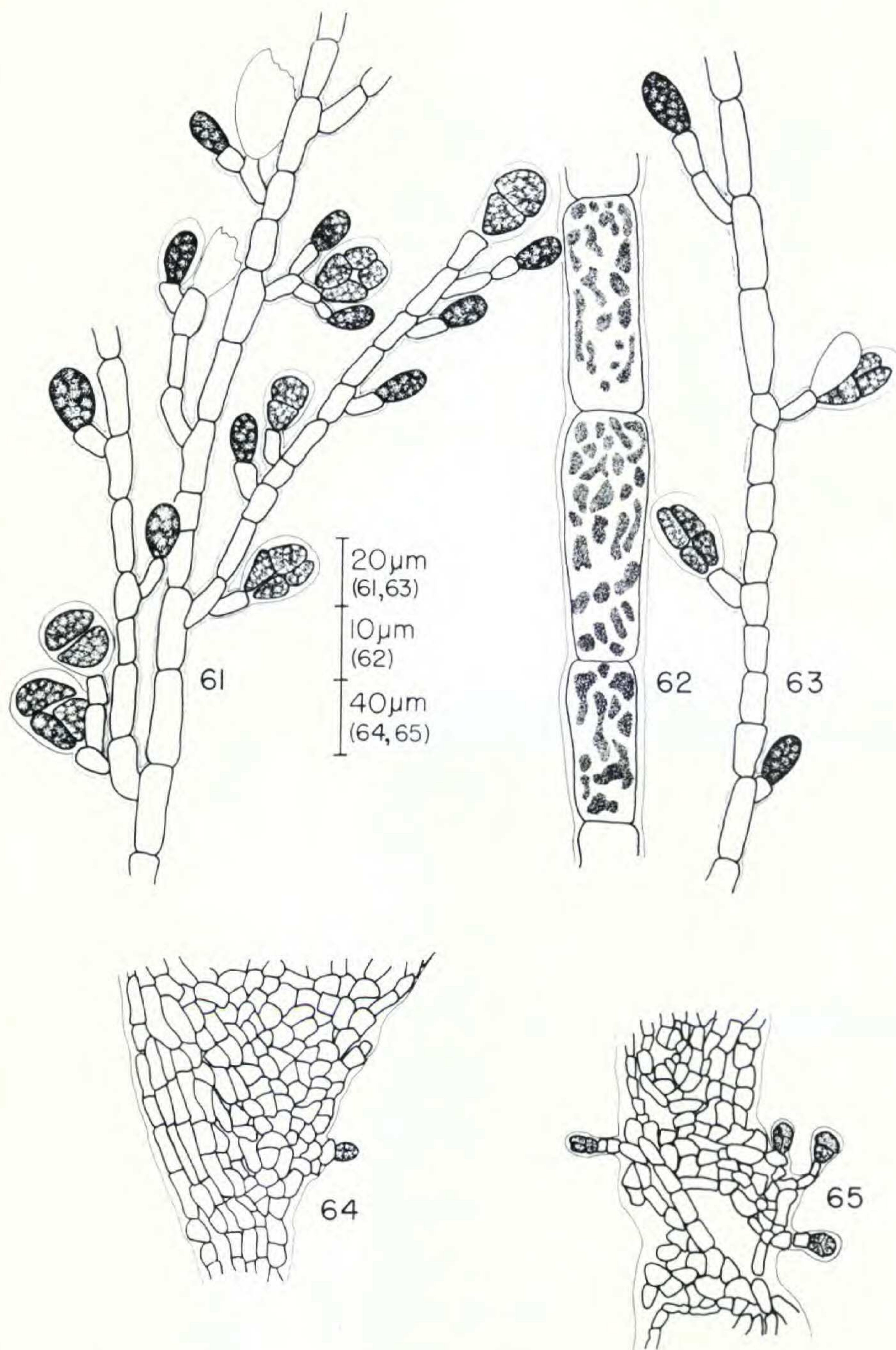
Figs. 44-45. *Audouinella unifila* (Jao) Woelk. Habit of two plants. MICH (Norton Point, Martha's Vineyard, 3. VIII. 1934, Jao, holotype).

Figs. 46-51. *Audouinella microscopica* (Naegeli In Kuetzing) Woelk. Habit of monosporangial plants. Figs. 46-47: MICH (Norton Point, Martha's Vineyard, 3. VIII. 1934, Jao, type of *Acrochaetium microfilum* Jao); Figs. 48-51: MICH (Black Rock, Sconticut Neck, New Bedford, Massachusetts, 25. VII. 1934, Jao, type of *Acrochaetium compactum* Jao).

Figs. 52-55: *Audouinella purpurea* (Lightfoot) Woelk. Fig. 52. Portion of erect system bearing carposporophytes. Figs. 53-55. Chromoplasts in cells of erect filaments. Figs. 52-55. WJW 3297 (Sandwich, Massachusetts, 22. I. 1971, Woelkerling).

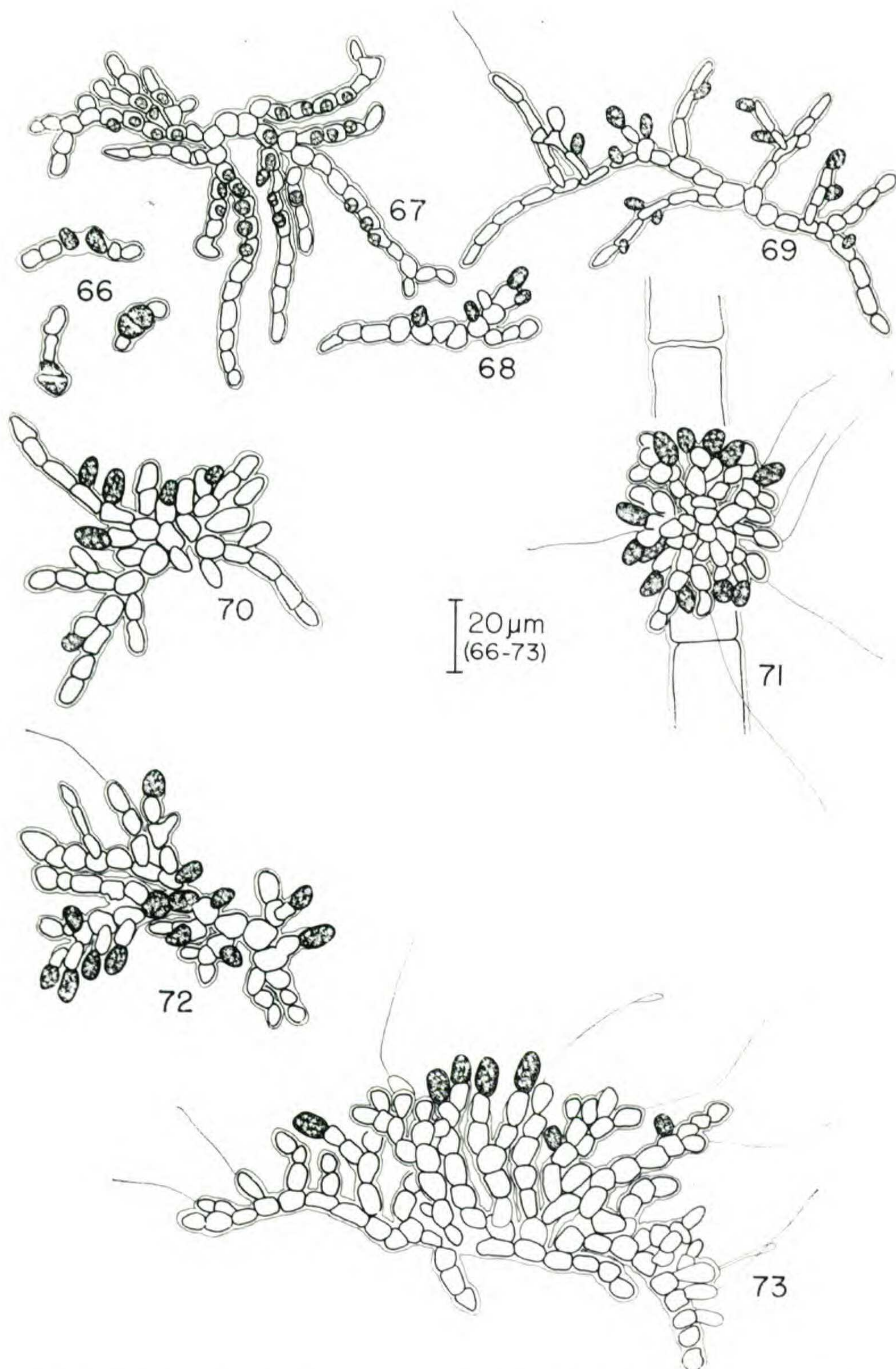


Figs. 56-60. *Audouinella saviana* (Meneghini) Woelk. Figs. 56-57. Prostrate systems. Fig. 58. Chromoplasts in cells of erect filaments. Figs. 59-60. Erect filaments bearing monosporangia (Fig. 59) and tetrasporangia (Fig. 60). Figs. 56-59: wjw 2753 (Woods Hole, Massachusetts, 21. VII. 1970, *Wilce*); Fig. 60: wjw 3818 (Sandwich, Massachusetts, 13. X. 1970, *Woelkerling*).

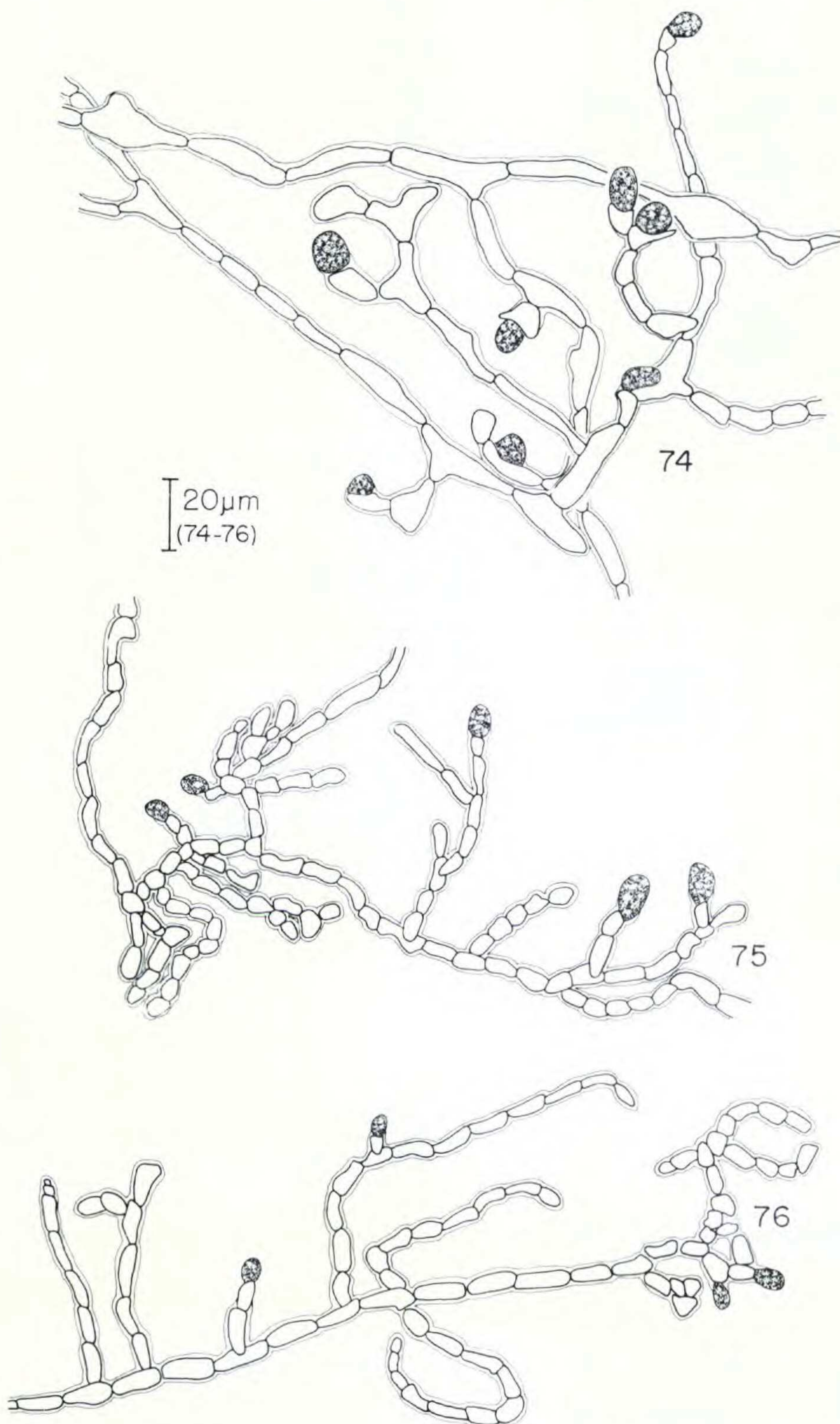


Figs. 61-63. *Audouinella spetsbergense* (Kjellman) Woelk. Figs. 61, 63. Erect filaments bearing tetrasporangia. Fig. 62. Chromoplasts in cells of erect filaments. Fig. 61: UPS (Fairhavn Island, Spitzbergen, 19. VIII. 1872, *Kjellman*, type of *A. spetsbergense*); Figs. 62, 63: UPS (Fairhavn Island, Spitzbergen, 12. VIII. 1872, *Kjellman*, type of *Rhodochorton penecilliforme*).

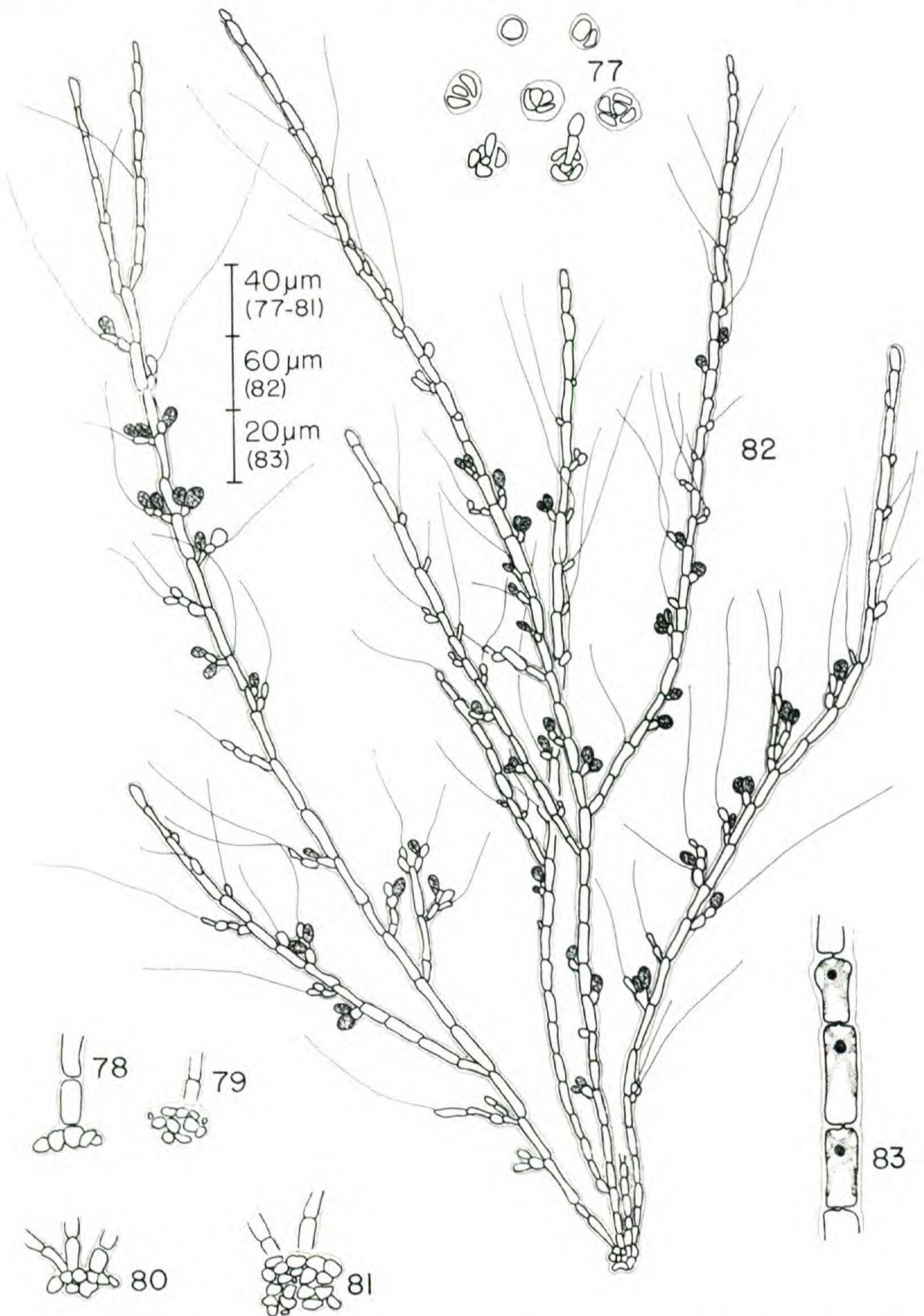
Figs. 64-65. *Caloconema membranacea* (Magnus) Woelk. Habit of portions of two plants. Note tetrasporangia (Fig. 65). Figs. 64-65: FH (Revere Beach, Massachusetts, 29. V. 1886, *Collins*, from Hauck and Richter 1888: 154).



Figs. 66-73. *Colaonema humilis* (Rosenvinge) Woelk. Fig. 66. Sporelings. Figs. 67-73. Habit of monosporangial plants. Figs. 66-69: MICH (Norton Point, Martha's Vineyard, Massachusetts, 3. VII. 1934, *Jao*, type of *Acrochaetium radiatum* *Jao*); Figs. 70, 72, 73: Edelstein 1382 (Ketch Harbor, Nova Scotia, 31. V. 1965, *Edelstein*); Fig. 71: WJW 1838 (Woods Hole, Massachusetts, 26. VI. 1969, *Conway*).



Figs. 74-76. *Colaonema minima* (Collins) Woelk. Habit of monosporangial plants. Note variation in shape of monosporangia and in cells subtending them. Fig. 74: wjw 2699 (Sandwich, Massachusetts, 30. VI. 1970, *Woelkerling*); Fig. 75: FH (Robinson's Hole, Elizabeth Islands, Massachusetts, VIII. 1907, *Collins*, type [= *Collins*, Holden, and Setchell 1908: 1493]); Fig. 76: C (Mollegrund, Denmark, 8. VIII. 1899, *Rosenvinge*, type of *Chantransia emergens* *Rosenvinge*).



Figs. 77-83. *Colaonema secundata* (Lyngbye) Woelk. Fig. 77. Sporelings showing characteristic parenchymatous grouping of cells. Figs. 78-81. Prostrate system of mature plants. Fig. 82. Habit of virgate plant. Fig. 83. Chromoplasts in cells of erect filaments. Fig. 77: wjw 2316 (Woods Hole, Massachusetts, 4. II. 1970, Woelkerling); Figs. 78-79, 82: wjw 2276 (West Falmouth, Massachusetts, 6. I. 1970, Woelkerling); Figs. 80-81: wjw 2476 (Nantucket Center, Massachusetts, 14. IV. 1970, Woelkerling); Fig. 83: wjw 2808 (Penikese Island, Massachusetts, 1. X. 1970, Woelkerling).

Table 1. Present status of audouinelloid taxa listed by Giard (1890), Hehre and Mathieson (1970), and Taylor (1957), (Author citations for taxa are recorded in the taxonomic treatments.)

<i>Name of Taxon in Older Literature</i>	<i>Present Status</i>
<i>Acrochaetium alcyonidae</i>	Conspecific with <i>Audouinella daviesii</i>
<i>A. amphiroae</i>	Conspecific with <i>A. daviesii</i>
<i>A. attenuatum</i>	See "Collections Inquirendae"
<i>A. dasyae</i>	<i>Audouinella dasyae</i>
<i>A. daviesii</i>	<i>Audouinella daviesii</i>
<i>A. emergens</i>	Conspecific with <i>Colaonema minima</i>
<i>A. flexuosum</i>	All New England collections referred to <i>Colaonema secundata</i>
<i>A. intermedium</i>	Conspecific with <i>Audouinella dasyae</i>
<i>A. microfilum</i>	Conspecific with <i>Audouinella microscopica</i>
<i>A. minimum</i>	<i>Colaonema minima</i>
<i>A. polyides</i>	See "Collections Inquirendae"
<i>A. radiatum</i>	Conspecific with <i>Colaonema humilis</i>
<i>A. sagraeanum</i>	See "Species Excludendae"
<i>A. thuretii</i>	Conspecific with <i>Audouinella saviana</i>
<i>A. zosterae</i>	Conspecific with <i>Audouinella dasyae</i>

Table 1 — Continued

<i>Audouinella efflorescens</i>	See "Collections Inquirendae"
<i>A. membranacea</i>	<i>Colaonema membranacea</i>
<i>Colaonema americana</i>	See "Species Inquirendae"
<i>Conchocelis rosea</i>	Referred to Bangiophycidae; not discussed in this account.
<i>Kylinia alariae</i>	<i>Audouinella alariae</i>
<i>K. compacta</i>	Conspecific with <i>Audouinella microscopica</i>
<i>K. hallandica</i>	Not recorded for New England and not discussed in this account
<i>K. moniliformis</i>	Conspecific with <i>Audouinella microscopica</i>
<i>K. secundata</i>	<i>Colaonema secundata</i>
<i>K. unifila</i>	<i>Audouinella unifila</i>
<i>K. virgatula</i>	Conspecific with <i>Colaonema secundata</i>
<i>Rhodochorton entozoicum</i>	See "Species Inquirendae"
<i>R. penicilliforme</i>	See "Collections Inquirendae" under <i>Audouinella spetsbergense</i>
<i>R. purpurea</i>	<i>Audouinella purpurea</i>

Name	No. erect Axes	Height	Cell diameter	Cell length	L/D	Spore Length	Spore Diameter
<i>Audouinella alariae</i> : Type, data from Jonsson 1901	1-2	500-1000 μ m	11-23 μ m below 7-11 μ m above	24-56 μ m below 20-72 μ m above	2-3 below 3-6 above	17-22 μ m	10-11 μ m
<i>Audouinella alariae</i> : Type, data from present study	1-3	—	11-18 μ m below 6-12 μ m above	25-60 μ m below 15-60 μ m above	2-4 below 2-6 above	15-20 μ m	10-12 μ m
<i>Chantransia rhipidandra</i> : Type, data from Rosenvinge	2-3	350 μ m	(7.5-) 9-11	—	2-3 (-4)	14-18 μ m	9-10 μ m
<i>Chantransia rhipidandra</i> : Type, data from this study	(1-) 2-3	450 μ m	7-13	20-40 μ m	2-4	15-18 μ m	9-11 μ m
<i>Audouinella alariae</i> : New England populations	1-2 (-3)	up to 1000 μ m	12-18 μ m below (4-) 7-10 (-15) μ m above	15-60 μ m below 15-65 μ m above	(1-) 1.5-4 below 2-6 (-9) above	12-20 μ m	8-12 μ m

Table 2. Data on Populations of *Audouinella alariae* and *Chantransia rhipidandra*.

	<i>A. dasyae</i>	<i>A. intermedium</i>	<i>A. zosterae</i>
Height	3 mm	2 mm	3 mm
Cell diameter	6-12 (-16) μm	8-10 μm [8-11 μm]	6.4-9.6 μm [6-11 μm]
Cell length	15-70 (-90) μm	(26-) 32-64 μm [15-70 μm]	32-70 μm [21-75 μm]
L/D	2-7 (-10)	— [2-7.5]	— [2-7]
Monospore length	16-24 μm	19-23 μm [16-20 μm]	22-31 μm [18-24 μm]
Monospore diameter	9-12 (-16) μm	9-13 μm [9-12 (-15) μm]	6.5-9.5 μm [8-11 μm]

Table 3. Data on populations of *A. dasyae* complex. Note: Data on *A. dasyae* is a composite of all New England collections examined. Data for *A. intermedium* and *A. zosterae* in brackets is based on personal studies of the types; data not in brackets is that reported by Jao (1936).

	<i>A. thuretii</i> (type)	<i>A. saviana</i> (type)	<i>A. saviana</i> (New England)
Height	up to 3 mm	up to 3 mm	up to 4 mm
Cell diameter	7-10 (-13) μm	7-12 μm	(7-) 8-12 (-14) μm
Cell length	20-45 μm	20-40 μm	20-60 μm
L/D	2-5	1.5-4	2-6 (-8)
Monospore length	15-20 μm	13-21 μm	18-27 μm
Monospore diameter	9-12 μm	8-12 μm	10-15 μm

Table 4. Data on populations of the *Audouinella saviana* complex. The first two columns represent data on type collection plants; the third is a composite of data on New England populations.

Collection	Cell Length	Cell Width	L/D	Spore Length	Spore Width
<i>Colaconema minima</i> (Collins data)	—	2-4 μ m	1-4 (-8)	7 μ m	5 μ m
<i>C. minima</i> (Woelkerling data)	4.5-15 μ m	3-7 μ m	1-4	6-11 μ m	3-6 μ m
<i>Chantransia emergens</i> (Rosenvinge data)	6-10.5 μ m	2-3.5 μ m	—	5-6.5 μ m	3-4 μ m
<i>C. emergens</i> (Woelkerling data)	7-12 μ m	3-6 μ m	1-4	6-10 μ m	3-5 μ m

Table 5. Data on Type Collections of *Colaconema minima* and *Chantransia emergens*.

Name	Cell length	Cell width	L/D	Spore length	Spore width
<i>Colaconema americana</i> type collection (Jao 1936)	(16-) 22-38 (-55) μ m	5-10 (-32) μ m	?	6-13 μ m	9.5-13 μ m
<i>Colaconema minima</i> WJW 2693	8-25 μ m	3-8 (-14) μ m	2-5	7-10 μ m	4-10 μ m
<i>Colaconema minima</i> WJW 2699	10-25 (-44) μ m	3-8 (-14) μ m	2-6	5-8 μ m	6-10 μ m

Table 6. Data on New England populations of *Colaconema* found in *Asparagopsis*. (Cell dimensions refer to prostrate system filaments.)

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